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A Scientific Review of the Potential Environmental Effects of Aquaculture in Aquatic Ecosystems

Volume IV:

The Role of Genotype and Environment in Phenotypic Differentiation Among Wild and Cultured Salmonids
(W.E. Tymchuk, R.H. Devlin and R.E. Withler);
Cultured and Wild Fish Disease Interactions in the Canadian Marine Environment
(A.H. McVicar, G. Olivier, G.S. Traxler, S. Jones, D. Kieser and A.-M. MacKinnon);
Trophic Interactions Between Finfish Aquaculture and Wild Marine Fish
(M. R.S. Johannes)

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FOREWORD

Context

The Government of Canada is committed to ensuring the responsible and sustainable development of the aquaculture industry in Canada. The Minister of Fisheries and Oceans' announcement of the $75 M Program for Sustainable Aquaculture (PSA), in August 2000, is a clear expression of this commitment. The objective of the PSA is to support the sustainable development of the aquaculture sector, with a focus on enhancing public confidence in the sector and on improving the industry's global competitiveness. Ensuring the sector operates under environmentally sustainable conditions is a key federal role.

As the lead federal agency for aquaculture, Fisheries and Oceans Canada (DFO) is committed to well-informed and scientifically-based decisions pertaining to the aquaculture industry. DFO has an ongoing program of scientific research to improve its knowledge of the environmental effects of aquaculture. The department is also engaged with stakeholders, provinces and the industry in coordinating research and fostering partnerships. As a contribution to the Federal government's Program for Sustainable Aquaculture, DFO is conducting a scientific review of the potential environmental effects of aquaculture in marine and freshwater ecosystems.

Goal and Scope

Known as the State-of-Knowledge (SOK) Initiative, this scientific review provides the current status of scientific knowledge and recommends future research studies. The review covers marine finfish and shellfish, and freshwater finfish aquaculture. The review focuses primarily on scientific knowledge relevant to Canada. Scientific knowledge on potential environmental effects is addressed under three main themes: effects of wastes (including nutrient and organic matter); chemicals used by the industry (including pesticides, drugs and antifoulants); and interactions between farmed fish and wild species (including disease transfer, and genetic and ecological interactions).

This review presents potential environmental effects of aquaculture as reported in the scientific literature. The environmental effects of aquaculture activities are site-specific and are influenced by environmental conditions and production characteristics at each farm site. While the review summarizes available scientific knowledge, it does not constitute a site-specific assessment of aquaculture operations. In addition, the review does not cover the effects of the environment on aquaculture production.

The papers target a scientific and well-informed audience, particularly individuals and organizations involved in the management of research on the environmental interactions of aquaculture. The papers are aimed at supporting decision-making on research priorities, information sharing, and interacting with various organizations on research priorities and possible research partnerships.

Each paper was written by or under the direction of DFO scientists and was peer reviewed by five experts. The peer reviewers and DFO scientists help ensure that the papers are up-to-date at the time of publication. Recommendations on cost-effective, targeted research areas will be developed after publication of the full series of SOK review papers.

State-of-Knowledge Series

DFO plans to publish 12 review papers as part of the SOK Initiative, with each paper reviewing one aspect of the environmental effects of aquaculture. This Volume contains 3 papers: The Role of Genotype and Environment in Phenotypic Differentiation Among Wild and Cultured Salmonids; Cultured and Wild Fish Disease Interactions in the Canadian Marine Environment; and Trophic Interactions Between Finfish Aquaculture and Wild Marine Fish.

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AVANT-PROPOS

Contexte

Le gouvernement du Canada est déterminé à assurer le développement responsable et durable de l'industrie aquacole au Canada. Le Programme d'aquaculture durable (PAD) de 75 millions de dollars annoncé par le ministre des Pêches et des Océans en août 2000 traduit clairement cet engagement. Ce programme vise à soutenir le développement durable du secteur aquacole, surtout en améliorant la confiance du public envers l'industrie et la compétitivité globale de celle-ci. Veiller à ce que l'industrie fonctionne dans des conditions durables sur le plan environnemental constitue une responsabilité essentielle du gouvernement fédéral. À titre d'organisme fédéral responsable de l'aquaculture, Pêches et Océans Canada (MPO) est déterminé à prendre des décisions éclairées qui reposent sur des données scientifiques éprouvées en ce qui concerne l'industrie aquacole. Le MPO mène un programme de recherches scientifiques pour améliorer ses connaissances sur les effets de l'aquaculture sur l'environnement. Le Ministère collabore également avec des intervenants, les provinces et l'industrie à la coordination des recherches et à l'établissement de partenariats. Le MPO contribue au Programme de l'aquaculture durable du gouvernement fédéral en passant en revue la littérature scientifique qui aborde les effets possibles de l'aquaculture sur les écosystèmes marins et d'eau douce.

Objectif et portée

Désignée projet sur l'état des connaissances, cette revue de la littérature définit l'état actuel des connaissances scientifiques sur les effets de l'élevage de poissons et de mollusques en mer et de la pisciculture en eau douce et fait des recommandations de recherches futures. La revue, qui se concentre surtout sur les connaissances scientifiques applicables au Canada, les aborde sous trois thèmes principaux : les impacts des déchets (éléments nutritifs et matière organique), les produits chimiques utilisés par l'industrie (pesticides, médicaments et agents antisalissures) et les interactions entre les poisons d'élevage et les espèces sauvages (transfert de maladies et interactions génétiques et écologiques).

Cette revue présente les effets environnementaux possibles de l'aquaculture documentés dans la littérature scientifique. Les effets environnementaux des activités aquacoles dépendent du site, des conditions environnementales et des caractéristiques de production de chaque établissement aquacole. L'examen résume les connaissances scientifiques disponibles mais ne constitue pas une évaluation des activités aquacoles spécifique au site. L'examen ne porte pas non plus sur les effets de l'environnement sur la production aquacole.

Les articles sont destinés à un auditoire de scientifiques et de personnes bien informées, notamment des personnes et des organisations participant à la gestion de la recherche sur les interactions environnementales de l'aquaculture. Les articles visent à soutenir la prise de décision sur les priorités de recherche, la mise en commun de l'information et les

interactions entre diverses organisations concernant les priorités de recherche et les partenariats de recherche possibles.

Rédigées par des scientifiques du MPO ou sous leur supervision, les articles ont été contrôlés par des pairs, ce qui assure qu'ils sont à jour au moment de leur publication. Après la publication de toute la série d'articles sur l'état des connaissances, des recommandations de recherches ciblées et rentables seront faites.

Série sur l'état des connaissances

Dans le cadre du projet de l'état des connaissances, le MPO prévoit publier douze articles de synthèse portant chacun sur un aspect des effets environnementaux de l'aquaculture. Le présent volume contient les trois articles suivants : Le rôle du génotype et de l'environnement dans la différenciation phénotypique chez les salmonidés sauvages et d'élevage ; interactions pathologiques entre les poissons saubages et d'élevage dans le milieu marin au Canada ; et interactions trophiques entre les poissons marins sauvages et d'élevage.

Renseignements supplémentaires

Pour de plus amples renseignements sur un article, veuillez communiquer avec son auteur principal. Pour de plus amples renseignements sur le projet de l'état des connaissances, veuillez communiquer avec :

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THE ROLE OF GENOTYPE AND ENVIRONMENT IN PHENOTYPIC DIFFERENTIATION AMONG WILD AND CULTURED SALMONIDS

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EXECUTIVE SUMMARY

This paper reviews the existing literature examining genetic influences on and consequences of the interaction between cultured and wild salmonids. The paper identifies major phenotypic changes that have occurred in domestic strains (e.g. morphology, physiology, and behavior), and examines whether these changes have effects on fitness in laboratory and natural environments. Long-term effects of interactions between domestic and wild strains will primarily arise from genetic effects, but the phenotype of domestic strains relative to wild strains arises from both genetic and environmental forces. Separating these causal components of phenotype is required to understand the potential effects of introgression events, yet achieving this goal remains a difficult task. Studies in the wild are required to fully determine the fitness of domestic and wild strains and thus examine potential long-term consequences arising from their interaction.

Genotype, in addition to environment, determines the adaptive phenotypic characteristics (i.e. reproductive capabilities and ongoing survival) of salmonids, and, as such, it is likely that disruption of this genetic structure may have short-term and long-term effects on individual fitness as well as the future resilience of populations to natural and anthropogenic pressures. Domestication has been noted to have a significant effect on life history traits in salmonids (Thorpe 2004). Domestication may select for many different traits, including improved growth rates, earlier age at maturity and spawning, greater survival, increased tolerance to high temperature and resistance to disease (Hynes et al. 1981). Differences between wild and cultured fish represent a phenotypic continuum, ranging from differences among natural strains, to differences between wild and sea-ranched fish, to differences between wild and highly selected domestic cultured fish (Figure 1). Alterations in fitness-related traits in hatchery fish should be typical of differences expected in aquacultured salmon, although the latter may show a greater magnitude of change due to an increased length of time under intentional and indirect selection, which is usually conducted in isolation from wild genetic pools. Accumulated evidence now indicates that some fitness-related traits affected by domestication, such as growth, competitive ability, and anti-predator behavior, are in part genetically controlled. Transgenic fish, which can be viewed as an extreme form of domestication,

are not considered in the present discussion except when examined as a model system for assessment of genotype/phenotype relationships (Devlin et al. 2001).

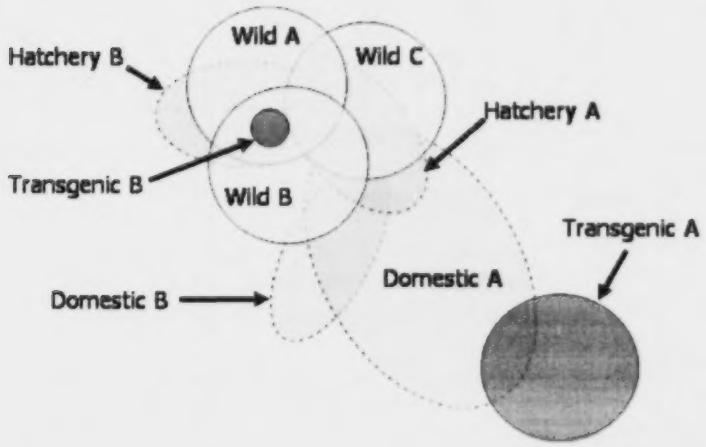

Figure 1. Representation of the relationships among phenotypic states for one hypothetical set of wild, hatchery, domestic, and transgenic strains. The ranges of phenotype observed among different wild populations are anticipated to overlap considerably with each other and with hatchery strains derived from them. Domestic strains that have undergone directed and unintentional selection are expected to possess phenotypes different from wild and hatchery populations, often in a common direction away from the wild phenotype, and in some cases to an extent seen for transgenic strains. Transgenic strains can possess a wide range of phenotypic transformations for novel traits, and for existing traits previously possessed by the host strain, or may have no change in phenotype from the host strain.

- ***Phenotypic differences between cultured and wild fish***

Rearing fish in a culture environment can lead to environmentally determined differences in morphology relative to those reared in the wild. The extent of these differences depends on the type and the length of time spent within the artificial environment, and the intensity of the culture conditions such as crowding, food supply, etc. Multiple generations of strains kept within the culture environment may lead to genetically based morphological differences arising from selection for traits affording fitness benefits in culture.

Domestication has also been shown to alter the physiology of fish. Environmental factors such as availability of food resources and temperature will of course have an effect on growth of fish. However, there can also be large differences in growth between

cultured and wild strains as a result of genetic differences between the strains. The magnitude of the growth differences caused by genotype will be dependent on the purpose and history of the cultured strain. Aquacultured strains that have been intensely selected for enhanced growth show a larger shift in growth phenotype from the founding line compared with those strains that have not experienced directed selection. It is important to note that it is often not clear whether physiological differences are a cause or consequence of other phenotypic differences between the strains (such as growth or behavior differences). It is therefore difficult to clarify whether physiological differences have a genetic basis per se, or if they are a product of the environment.

Behavioral differences commonly arise during domestication. Cultured and wild fish do show differences in the level of aggression displayed towards conspecifics, although there has not been a consistent trend as to whether aggression increases or decreases under culture. A common assertion is that aggression will decrease under culture when fish are reared in crowded conditions and do not have to fight for limited food resources. A genetically determined reduced response to predators seems to be a consistent trend in domestic strains across several species. In contrast, little research has been conducted to reveal genetic control of foraging strategy, habitat selection, and dispersal. A genetic basis for altered foraging strategy could arise from phenotypic expression of other genetically influenced traits such as growth or morphology, which would drive foraging behavior characteristics.

Expression of physiological and behavioral phenotypes will ultimately determine survival. Survival is influenced by most other phenotypic traits, and the environment in which they are expressed. Cultured fish, either through a plastic response to their environment or through an adaptive response to altered selection pressures, tend to express phenotypic characteristics best suited for the culture environment. Consequently, they tend to have a lower survival than wild fish in a natural environment. However, few studies have examined whether cultured fish that experience a natural environment throughout their life history will still show decreased survival relative to the wild fish. Furthermore, the strength of the genetic basis of survival is not known, nor is it clear whether cultured fish still have the ability to show a phenotypically plastic response to the environment that will maximize their ability to survive.

Reproductive capabilities of domesticated fish are often affected. The literature consistently observes that cultured fish often have the physiological ability to spawn, but that altered spawning behavior limits their success. While the reproductive success of farmed fish may be low, the potential for significant gene flow still exists because the population of farmed fish often outnumbers the population of resident wild fish (at least in the case for Atlantic salmon), at times by as much as 3:1 (Lund et al. 1994; Lura and Økland 1994). There are no data comparing the ability of farmed and wild Pacific salmon to spawn in nature, but comparisons between hatchery and wild coho salmon, and studies examining cultured wild strains indicate that trends observed for Atlantic salmon may be typical of the phenotypic changes expected during domestication.

Genetic effects of farmed fish on wild populations would depend in part on the reproductive behavior of farmed fish in the wild. Evidence suggests that farmed fish have the ability to breed successfully in the wild, although contradicting results exist. There are generally significant differences in breeding potential between cultured and wild fish (Fleming and Gross 1992, 1993; Fleming et al. 1996; Berejikian et al. 1997; Bessey et al.

2004), although other studies have found similar reproductive success for hatchery and native fish in the wild (Dannewitz et al. 2004; Palm et al. 2003). Morphology and life history traits related to reproductive behavior respond evolutionarily to altered selection regime in the hatchery environment (Fleming 1994; Fleming and Gross 1989). The genetic effect of aquacultured salmon on wild populations will depend not only on the size of the wild population, but also on variation in breeding success (Fleming and Petersson 2001).

- ***Cause of phenotypic differentiation between cultured and wild strains***

Phenotypic differences between farmed and wild salmonids may arise from a combination of genetic and environmental effects, but in most cases, the origin of the difference is not well defined. Environmentally based phenotypic differences would not be passed to offspring as they do not have a genetic basis, and are thus anticipated to have single generation effects arising directly from escaped fish. In contrast, genetic differences have the potential to affect the wild populations of a species over a longer time frame. Thus, it is therefore critical to separate the influence of genotype and environment.

To assess genetic effects, experiments must be performed by rearing fish of different origins in a common environment (i.e. common-garden experiments.). Such experiments can help determine whether cultured fish have an altered genotype that has arisen in response to selection pressures from an artificial environment. Environmental effects (i.e. phenotypic plasticity) can be tested by rearing fish of a common genetic background in different environments, revealing whether phenotypic plasticity (Hutchings 2004) may have altered phenotype in response to the environmental conditions.

Currently, there is still limited knowledge on how the environment will act on inherent genetic differences among strains (i.e. will environmental conditions affect different genotypes in distinct ways through genotype x environment interactions). For example, fast-growing domestic fish may have a greater growth advantage relative to wild fish under culture conditions than they do in nature. An understanding of genotype by environment interactions remains one of the most critical components influencing phenotype and fitness. Research in this area is required to improve prediction of genetic effects arising from interaction between wild and cultured fish.

- ***Mechanism of genetic interaction***

Genetic effects of domestic fish may be direct or indirect. Direct genetic effects include the alteration of the wild genome (introgression) as a result of interbreeding between wild and domesticated fish, or the production of sterile hybrids. Indirect effects include the effect of reduced effective population size or altered selection pressure arising from competition or the introduction of pathogens (Krueger and May 1991; Skaala et al. 1990; Waples 1991). Genetic effects of hybridization between farmed and wild salmon are somewhat unpredictable and may differ between populations, but most interactions have been generally found to be disadvantageous when the genetic effects alter fitness-related traits (Hindar et al. 1991). Most studies have focused on the fitness of the F_1 generation when exploring the effects of interbreeding between domestic and wild strains. While such hybrids may have enhanced fitness due to hybrid vigor, the

negative effects of outbreeding depression are not manifested until F_2 and later generations, and thus simple first-generation hybrid studies have limited predictive value.

The genetic effect of escaped cultured fish on wild populations will also depend on the demographic of the wild population, the magnitude and frequency of the escape, and the extent of introgression of aquacultured genotypes into the wild population (Hutchings 1991). The phenotype of wild and farmed hybrids may vary depending on the source and genetic structure of the wild population (e.g., see Einum and Fleming 1997). Anadromous populations of salmonids may be somewhat resistant to introgression due to aspects of their complex life histories such as overlapping maturation age classes and straying among distinct populations (Utter and Epifanio 2002). Furthermore, genetic distance between the two populations does not seem to be a reliable indicator of the potential effects of introgression (Utter and Epifanio 2002).

KNOWLEDGE GAPS AND RECOMMENDATIONS

- ***More fully define the genetic basis of domestic traits and the mechanisms by which they alter phenotype.***

It is clear that phenotypic differences (particularly growth) between cultured and wild fish are due in part to altered genotype. However, the specific genetic changes that have occurred to cause these phenotypic differences are not yet understood. For example, traits that are controlled by many alleles of small effect will present different risks to wild populations and will require different management strategies relative to traits that are caused by a small number of alleles of large effect. A better understanding of the genetic changes underlying desired traits will also aid in the development of custom aquaculture strains through the use of marker-assisted selection. Such genetic information may be obtained from: 1) additional breeding studies (e.g. assessing heteritabilities for critical traits in wild and cultured populations under culture and natural conditions, and the scale to which outbreeding depression and/or heterosis are at play among populations); 2) experiments mapping and identifying genes and alleles responsible for specific phenotypes; and, 3) gene expression studies identifying candidate genes involved in fitness-related processes.

- ***Determine whether conserved genetic and physiological pathways are employed among domestic strains to achieve alteration of specific trait.***

Further to the above, it will be crucial to assess whether genetic changes arising through the process of domestication are a conservative process. There has been little comparison among strains and species of cultured fish to determine if the genetic alterations leading to phenotypic differences occur in predictable patterns, or if each strain is developed through a unique set of alleles. This information will determine whether a general risk management strategy could be generalized, or if plans must be developed on a case-by-case basis.

- ***Extensive research is required to determine which environmental variables play controlling roles in influencing the magnitudes of phenotypic differences among wild and between wild and domestic strains (i.e. improve our knowledge of phenotypic plasticity and genotype x environment interactions).***

Because of the difficulty of making observations in natural environments, there are few studies that test whether differences among strains observed in an artificial environment are an accurate predictor of the characteristics that will be displayed in the natural environment. Thus, there is a need for more rigorous assessments of the plasticity of cultured and wild strains to assess whether domestic genotypes have response to environmental conditions which differ from wild type in non-parallel ways (i.e. genotype x environment interactions). This area of research is critical.

- ***Undertake experiments to evaluate the contribution of phenotypic differences between domestic and wild strains to survival and reproductive fitness.***

Altering the expression of a phenotypic trait can alter overall fitness. Different phenotypic traits will interact in a complex manner to determine the fitness of an individual. While there is much literature on discrete phenotypic differences among cultured and wild strains, there is a need for more complex analyses of how these differences interact during the life history of the fish and consequently influence their ability to survive and reproduce.

- ***Fitness evaluations must be undertaken in nature to provide information to reliably predict net fitness and consequences of domestic genotypes introgressed into wild populations. Without data from nature, laboratory experiments may reveal forces causing phenotypic and fitness differences, but their true magnitudes cannot be known with certainty.***

It is critical to extend laboratory studies and assess identified genetic differences such that true determinations of their influence on fitness in nature can be determined. It will also be important to examine the ability and the rate that populations may be able to revert to naturally selected genotypes and phenotypes following introgression events.

- ***Given current uncertainty in our ability to a priori predict consequences of introgression, research directed to monitoring and minimizing interactions should be supported.***

The outcome of genetic interaction between farmed and wild populations is difficult to predict as our understanding of genetic dynamics is poorly developed for age-structured populations with overlapping generations such as those shown by salmonid populations. Consequently, conservative approaches have been recommended when assessing genetic effect risks (Ryman 1997; Waples 1991). Clearly, an important first step is to minimize escape of cultured fish into the wild (Altukhov and Salmenkhova 1990; Krueger and May 1991). Effort should also be directed at developing molecular techniques to better identify and monitor introgression of cultured strains into wild populations, particularly for reproductively mature stages and consequent early stages of their progeny. The use of triploid fish or other containment techniques in aquaculture may eliminate genetic

effects, and reduce the ecological consequences of escaped farmed fish on wild stocks (Cotter et al. 2000; Devlin and Donaldson 1992).

- ***Develop models that make use of the emerging understanding of the relationship between genotype, phenotype and fitness to allow prediction of the consequences of introgression of domestic and wild strain.***

Recent research has revealed that many phenotypic traits that differ between wild and domestic strains are controlled by additive genetic variation (Tymchuk et al. 2006, McGinnity et al. 1997, 2003, Fleming et al. 2000). These observations could now allow estimation of the effects of introgression on the genotype of wild populations, assuming neutral fitness. Further, modeling exercises can allow sensitivity analysis to estimate risk arising from different genotypes under various introgression scenarios, and, coupled with studies of natural fitness among genotypes, may be used in the future to predict consequences in the wild.

LE RÔLE DU GÉNOTYPE ET DE L'ENVIRONNEMENT DANS LA DIFFÉRENCIATION PHÉNOTYPIQUE CHEZ LES SALMONIDÉS SAUVAGES ET D'ÉLEVAGE

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SOMMAIRE

L'objectif du présent document est d'examiner les ouvrages qui traitent des influences génétiques sur les interactions entre les salmonidés d'élevage et sauvages et sur les conséquences de ces interactions. Sont mis en évidence dans ce document les principaux changements phénotypiques qui sont survenus dans les souches domestiques (p. ex. sur le plan de la morphologie, de la physiologie et du comportement). Ce document comprend également un examen visant à déterminer si ces changements ont des effets sur la valeur adaptative en laboratoire et en milieu naturel. Les effets à long terme des interactions entre les souches d'élevage et sauvages découlent principalement d'effets génétiques, tandis que le phénotype des souches domestiques, par rapport à celui des souches sauvages, découle de conditions génétiques et environnementales. La distinction de ces composants qui déterminent le phénotype est nécessaire pour comprendre les effets possibles d'introgressions, mais elle demeure difficile à faire. Les études menées sur le terrain sont essentielles afin de bien déterminer la valeur adaptative des souches domestiques et sauvages, ce qui permet d'examiner les conséquences à long terme possibles des interactions entre ces souches.

Le génotype, en plus du milieu, détermine les caractéristiques phénotypiques adaptatives (c.-à-d. capacités de reproduction et de survie) des salmonidés, et, de ce fait, il est probable que la perturbation de cette structure génétique ait des effets à court et long termes sur la valeur adaptative des individus ainsi que sur la résilience des populations face aux contraintes d'origine naturelle et anthropogénique. Thorpe (2004) a montré que la domestication a un effet considérable sur des caractéristiques du cycle vital des salmonidés. La domestication comprend une sélection parmi de nombreux caractères, notamment un meilleur taux de croissance, une maturité et une capacité de reproduction en plus bas âge, un meilleur taux de survie, une plus grande tolérance aux températures élevées et une plus grande résistance aux maladies (Hynes et al., 1981). Les différences entre les poissons d'élevage et sauvages constituent une série phénotypique homogène et s'étendent des différences entre souches naturelles aux différences entre les poissons sauvages et les poissons d'élevage ayant fait l'objet d'une sélection poussée, en passant par les différences entre les poissons sauvages et les poissons élevés en mer (figure 1). Les modifications de caractères liés à la valeur adaptative chez les poissons

d'élevage devraient être typiques des différences attendues chez le saumon d'élevage, bien que ce dernier puisse présenter des changements plus importants en raison de la période plus longue au cours de laquelle il fait l'objet d'une sélection intentionnelle ou indirecte, celle-ci étant habituellement menée dans un milieu sans ressource génétique sauvage. Il existe maintenant un ensemble de preuves à l'appui de l'hypothèse voulant que certains caractères liés à la valeur adaptative et touchés par la domestication, notamment la croissance, la capacité compétitive et le comportement d'évitement des prédateurs, soient en partie déterminés par des facteurs génétiques. Les poissons transgéniques, qui peuvent être perçus comme une forme extrême d'animaux domestiques, ne sont pas pris en considération dans la présente discussion sauf quand ils sont examinés en tant que système modèle pour l'évaluation des relations entre le génotype et le phénotype (Devlin et al., 2001).

- ***Différences phénotypiques entre les poissons d'élevage et les poissons sauvages***

La morphologie des poissons peut varier en fonction du milieu où ils ont été élevés (artificiel ou naturel). L'ampleur des différences varie selon l'espèce concernée, la période de temps passée en milieu artificiel et l'intensité de l'élevage (comme l'entassement, l'approvisionnement en nourriture, etc.). La conservation de multiples générations de souches dans un milieu de culture peut donner lieu à des différences morphologiques d'origine génétique dues à la sélection de caractères améliorant la valeur adaptative en milieu d'élevage.

Il a également été démontré que la domestication entraîne des modifications de la physiologie des poissons. Le milieu a évidemment un effet sur la croissance des poissons en raison de facteurs comme la disponibilité des ressources alimentaires et la température. Cependant, des différences génétiques peuvent également entraîner de grandes différences sur le plan de la croissance entre les souches d'élevage et les souches sauvages. L'importance de ces différences de croissance dues au génotype dépend de la fonction de la souche d'élevage et de son historique. L'écart entre le phénotype de croissance des souches d'élevage et celui de leur souche d'origine est beaucoup plus important dans le cas des souches d'élevage qui ont fait l'objet d'une sélection intensive aux fins d'amélioration de la croissance que dans le cas des souches qui n'ont pas fait l'objet d'une sélection dirigée. Il est important de souligner qu'il est souvent difficile de déterminer si des différences physiologiques entre deux souches sont une cause ou une conséquence d'autres différences phénotypiques entre celles-ci (comme dans le cas des différences de croissance ou de comportement). Il est par conséquent difficile d'établir si les différences physiologiques ont un fondement génétique en soi ou si elles sont un produit du milieu.

Des différences de comportement surviennent généralement lors de la domestication. Les poissons d'élevage diffèrent des poissons sauvages quant au degré d'agressivité à l'égard de leurs congénères, mais aucune tendance constante n'a été observée jusqu'à maintenant quant à savoir si l'agressivité augmente ou diminue chez les poissons d'élevage. Une assertion couramment formulée veut que l'agressivité diminue en milieu d'élevage quand l'entassement est élevé et que les poissons n'ont pas à lutter pour les ressources alimentaires. Une réponse réduite aux prédateurs déterminée par le génotype semble être une constante chez les souches domestiques de plusieurs espèces. En comparaison, peu de recherches ont été menées afin de déterminer l'influence du

génotype sur la stratégie d'alimentation, le choix de l'habitat et la dispersion. Une modification d'origine génétique de la stratégie d'alimentation pourrait découler de l'expression phénotypique d'autres caractères influencés par des facteurs génétiques, comme la croissance ou la morphologie, qui détermineraient les caractéristiques du comportement d'alimentation.

L'expression de phénotypes comportementaux et physiologiques constitue en bout de ligne un facteur déterminant de la survie. La survie dépend de la plupart des autres caractères phénotypiques ainsi que du milieu dans lequel ceux-ci sont exprimés. Les poissons d'élevage, par le biais de leur plasticité ou d'une réponse adaptative à des pressions sélectives modifiées, ont tendance à exprimer les caractères phénotypiques les mieux adaptés au milieu d'élevage. Par conséquent, leur taux de survie en milieu naturel a tendance à être inférieur à celui des poissons sauvages. Peu d'études ont cependant été menées afin de déterminer si les poissons d'élevage qui vivent dans un milieu naturel toute leur vie ont également un taux de survie inférieur à celui des poissons sauvages. De plus, nous ne connaissons pas l'importance du fondement génétique de la survie ni si les poissons d'élevage ont encore la capacité d'adapter leur phénotype au milieu afin de maximiser leur capacité de survie.

La domestication a souvent une incidence sur la capacité de reproduction des poissons. Les poissons d'élevage sont souvent physiologiquement aptes à se reproduire, mais toute modification de leur comportement de fraie limite leur succès. Même si le succès de reproduction des poissons d'élevage est faible, le potentiel d'un flux de gènes important existe toujours puisque l'effectif des populations de poissons d'élevage dépasse souvent l'effectif des populations de poissons sauvages résidents (c'est le cas au moins pour le saumon atlantique), parfois selon un rapport de 3 pour 1 (Lund et al., 1994; Lura et Økland, 1994). Nous ne possédons aucune donnée sur la capacité du saumon du Pacifique sauvage et d'élevage de se reproduire dans la nature, mais des comparaisons entre les saumons cohos d'élevage et sauvages et des études sur les souches sauvages cultivées indiquent que les tendances observées chez le saumon atlantique pourraient être typiques des changements phénotypiques attendus lors de la domestication.

Les effets génétiques des poissons d'élevage sur les populations sauvages dépendent en partie du comportement de reproduction des poissons d'élevage en milieu naturel. Des études suggèrent que les poissons d'élevage ont la capacité de se reproduire avec succès dans la nature, mais d'autres études montrent plutôt le contraire. Il y a habituellement des différences importantes entre le potentiel de reproduction des poissons d'élevage et celui des poissons sauvages (Fleming et Gross, 1992; Fleming et Gross, 1993; Fleming et al., 1996; Berejikian et al., 1997; Bessey et al., 2004), bien que les résultats de certaines études montrent que le succès de reproduction des deux types de poissons est semblable en milieu naturel (Dannewitz et al., 2004; Palm et al., 2003). Les caractères morphologiques et les caractéristiques du cycle vital liés au comportement de reproduction évoluent en fonction des changements de régime de sélection dans le milieu d'élevage (Fleming, 1994; Fleming et Gross, 1989). L'effet génétique des saumons d'élevage sur les populations sauvages dépend non seulement de la taille des populations sauvages, mais également des différences sur le plan du succès de reproduction (Fleming et Petersson, 2001).

- ***Cause des différences phénotypiques entre les souches d'élevage et les souches sauvages***

Les différences phénotypiques entre les salmonidés d'élevage et sauvages peuvent découler d'une combinaison d'effets environnementaux et génétiques, mais leur origine est le plus souvent mal définie. Les différences phénotypiques dues au milieu ne sont pas transmises à la progéniture puisqu'elles n'ont pas de fondement génétique. Il convient par conséquent de s'attendre à ce qu'elles aient des effets qui touchent une génération seulement et qui découlent directement de poissons évadés. En comparaison, les différences génétiques ont le potentiel d'avoir des effets à plus long terme sur les populations sauvages d'une espèce. Il est par conséquent crucial de distinguer les effets génétiques des effets environnementaux.

Les effets génétiques peuvent être évalués dans le cadre d'expériences d'élevage de poissons d'origine différente dans un même milieu (c.-à-d. expériences dans des conditions semblables en laboratoire), ce qui permet de déterminer si le génotype des poissons d'élevage peut être modifié par le biais de pressions sélectives en milieu artificiel. Les effets environnementaux (c.-à-d. plasticité phénotypique) peuvent être analysés en élevant des poissons d'un même patrimoine génétique dans des milieux différents (Hutchings, 2004).

À l'heure actuelle, les connaissances sur l'incidence du milieu sur les différences génétiques inhérentes entre souches sont limitées (c.-à-d. est-ce que l'incidence des conditions environnementales varie en fonction des génotypes en raison d'interactions génotype et environnement). Par exemple, l'avantage compétitif au chapitre de la croissance des poissons domestiques à croissance rapide, par rapport aux poissons sauvages, peut être plus grand en milieu artificiel qu'en milieu naturel. Les interactions génotype et environnement demeure un des facteurs les plus importants qui ont une incidence sur le phénotype et la valeur adaptative. Par conséquent, il est nécessaire de mener des recherches dans ce domaine afin d'améliorer les prévisions des effets génétiques qui découlent des interactions entre les poissons d'élevage et les poissons sauvages.

- ***Mécanisme d'interaction génétique***

Les effets génétiques des poissons domestiques peuvent être directs ou indirects. Les effets directs comprennent les modifications du génome sauvage (introgressions) dues au croisement de poissons d'élevage et de poissons sauvages, ou la production d'hybrides stériles. Les effets indirects comprennent l'effet d'une baisse de la taille effective d'une population ou d'une modification d'une pression sélective qui découle de la concurrence ou de l'introduction d'agents pathogènes (Krueger et May, 1991; Skaala et al., 1990; Waples, 1991). Les effets génétiques du croisement de saumons sauvages et de saumons d'élevage sont un peu imprévisibles et peuvent varier entre les populations, mais la plupart des interactions se révèlent généralement être désavantageuses quand les effets génétiques modifient les caractères liés à la valeur adaptative (Hindar et al., 1991). La plupart des études ont porté sur la valeur adaptative de la génération F_1 lors de l'examen des effets de croisements de souches domestiques et sauvages. Les hybrides ainsi produits peuvent avoir une valeur adaptative accrue en raison de l'hétérosis, mais les effets négatifs de la dépression due à des croisements distants n'apparaissent qu'à

partir de la deuxième génération. Les études simples sur les hybrides de première génération ont donc une valeur prédictive limitée.

Les effets génétiques des poissons d'élevage évadés sur les populations sauvages dépendent également des aspects démographiques de ces populations, de l'ampleur et de la fréquence des évasions, et de l'ampleur des introgressions de gènes de souches d'élevage chez les populations sauvages (Hutchings, 1991). Le phénotype d'un hybride d'un poisson d'élevage et d'un poisson sauvage peut varier en fonction de l'origine et de la structure génétique de la population du poisson sauvage (voir par exemple Einum et Fleming, 1997). Les populations de salmonidés anadromes peuvent être quelque peu résistantes à l'introgression en raison de particularités de leur cycle biologique complexe, comme les classes d'âge qui se chevauchent sur le plan de la maturation et l'errance d'individus entre populations distinctes (Utter et Epifanio, 2002). La distance génétique entre deux populations ne semble pas constituée un indice fiable des effets potentiels d'une introgression (Utter et Epifanio, 2002).

LACUNES DANS LES CONNAISSANCES ET RECOMMANDATIONS

- ***Définir de façon plus approfondie le fondement génétique des caractères des poissons domestiques et les mécanismes grâce auxquels ces caractères modifient le phénotype.***

Il est évident que les différences phénotypiques (en particulier sur le plan de la croissance) entre les poissons d'élevage et sauvages sont au moins en partie dues à des différences génétiques. Les changements génétiques particuliers qui sont responsables de ces différences phénotypiques demeurent toutefois inconnus. Par exemple, les caractères qui sont déterminés par un grand nombre d'allèles aux effets peu importants, par rapport aux caractères qui découlent d'un petit nombre d'allèles aux effets importants, présentent des risques différents pour les populations sauvages et rendent nécessaires des stratégies de gestion différentes. Une meilleure compréhension des changements génétiques qui sous-tendent les caractères désirés contribuera également à l'élaboration de souches d'élevage sur mesure grâce à une sélection à l'aide de marqueurs. De telles informations génétiques peuvent être obtenues dans le cadre d'études de reproduction approfondies (p. ex. évaluation de l'héritabilité des caractères essentiels chez les populations d'élevage et sauvages dans des conditions naturelles ou artificielles et évaluation de l'importance de la dépression due à des croisements distants ou de l'hétérosis au sein des populations), d'expériences de cartographie et d'identification des gènes et allèles responsables de certains phénotypes et d'études sur l'expression génique visant à relever les gènes nécessaires aux processus liés à la valeur adaptative.

- ***Déterminer si les voies physiologiques et génétiques conservées sont utilisées chez les souches domestiques pour modifier un caractère particulier.***

En continuité avec le point précédent, il est crucial d'évaluer si les changements génétiques qui découlent du processus de domestication constituent un processus prudent. Les souches et les espèces de poissons d'élevage ont fait l'objet de peu de comparaisons afin de déterminer si les changements génétiques qui entraînent des différences phénotypiques se produisent de façon prévisible ou si chaque souche est le

résultat d'un ensemble unique d'allèles. Ces renseignements permettront de déterminer si une stratégie de gestion du risque peut être généralisée ou si des plans doivent être élaborés au cas par cas.

- ***Une recherche approfondie est nécessaire pour déterminer quelles variables environnementales ont une incidence importante sur l'ampleur des différences phénotypiques chez les souches sauvages et domestiques et entre celles-ci (c.-à-d. améliorer nos connaissances sur la plasticité phénotypique et les interactions génotype et environnement).***

Puisqu'il est difficile de procéder à des observations en milieu naturel, peu d'études visent à déterminer si les différences entre souches observées en milieu artificiel constituent un moyen de prévoir avec exactitude les caractères exprimés en milieu naturel. Des évaluations plus rigoureuses de la plasticité des souches d'élevage et sauvages sont donc nécessaires afin de déterminer si la réponse des génotypes domestiques aux conditions environnementales diffère de celle des génotypes sauvages de façons non parallèles (c.-à-d. interactions génotype et environnement). Ce domaine de recherche est crucial.

- ***Entreprendre des études visant à évaluer la contribution des différences phénotypiques entre souches sauvages et domestiques à la survie et au succès de reproduction.***

La modification de l'expression d'un caractère phénotypique peut avoir des répercussions sur la valeur adaptative d'un individu, cette valeur étant déterminée par différents caractères phénotypiques aux interactions complexes. Il existe de nombreux ouvrages sur les différences phénotypiques distinctes entre les souches sauvages et d'élevage, mais des analyses plus approfondies sont nécessaires afin de déterminer les interactions entre ces différences au cours du cycle de vie des poissons ainsi que l'incidence de ces différences sur les capacités de survie et de reproduction.

- ***Des évaluations de la valeur adaptative doivent être menées en milieu naturel afin d'obtenir des données permettant de prévoir de façon fiable la valeur adaptive nette et les conséquences de l'introgression de gènes de souches domestiques chez des populations sauvages. Les expériences en laboratoire peuvent révéler des facteurs à l'origine des différences phénotypiques et des différences sur le plan de la valeur adaptative, mais il est impossible de déterminer avec certitude la véritable importance de ces facteurs sans donnée obtenue en milieu naturel.***

Des études plus poussées en laboratoire et l'évaluation des différences génétiques identifiées sont essentielles pour que les effets de ces différences sur la valeur adaptative puissent être déterminés. Il est également important d'examiner la capacité des populations à revenir à un génotype et à un phénotype sélectionnés naturellement à la suite d'une introgression et de déterminer le taux auquel les populations peuvent y parvenir.

- ***Compte tenu de l'incertitude actuelle quant à notre capacité de prévision a priori des conséquences d'une introgression, les recherches axées sur la surveillance des interactions et sur la réduction au minimum de celles-ci devraient être appuyées.***

Le résultat des interactions génétiques entre populations sauvages et d'élevage est difficile à prévoir puisque notre compréhension de la dynamique génétique est peu approfondie en ce qui a trait aux populations structurées selon l'âge et caractérisées par des générations chevauchantes, comme les populations de salmonidés. Par conséquent, des approches prudentes ont été recommandées aux fins d'évaluation des risques d'effets génétiques (Ryman, 1997; Waples, 1991). Il est évident que la réduction au minimum des évasions de poissons d'élevage constitue une première étape importante (Altukhov et Salmenkhova, 1990; Krueger et May, 1991). Des travaux devraient également porter sur l'élaboration de techniques moléculaires visant à faciliter l'identification et la surveillance des introgressions de gènes de souches d'élevage chez des populations sauvages, particulièrement en ce qui a trait aux poissons matures et aux premiers stades de leur progéniture. L'utilisation de poissons triploïdes ou d'autres techniques de confinement en aquaculture peut permettre d'éliminer les effets génétiques et de réduire les conséquences écologiques des évasions de poissons d'élevage pour les stocks sauvages (Cotter et al., 2000; Devlin et Donaldson, 1992).

- ***Élaborer des modèles qui utilisent les nouvelles connaissances sur la relation entre le génotype, le phénotype et la valeur adaptative pour prévoir les conséquences d'introgressions chez des souches sauvages et domestiques.***

Des recherches récentes ont révélé que nombre de caractères phénotypiques qui diffèrent entre les souches sauvages et domestiques sont déterminés par des variations génétiques additives (Tymchuk et al., 2005; McGinnity et al., 1997 et 2003; Fleming et al., 2000). Ces observations font en sorte qu'il est maintenant possible d'estimer les effets d'une introgression de gènes chez des populations sauvages si l'on suppose que la valeur adaptative demeure la même. De plus, les essais de modélisation rendent possible des analyses de sensibilité afin d'estimer le risque lié à différents génotypes dans divers scénarios d'introgression, et, lorsque combinés à des études sur la valeur adaptative naturelle de génotypes, ces essais pourront être utilisés pour prévoir les conséquences en milieu naturel.

INTRODUCTION

Demand for food from a burgeoning human population, coupled with natural and anthropogenic environmental effects on wild fish stocks, is shifting focus on seafood supply from natural fisheries to aquaculture and hatchery programs. This trend is global. In 2001 aquaculture accounted for approximately 37.4% (59.7 million metric tons) of the world's food supply from aquatic sources (FAO 2006). In Canada in 2002, aquaculture accounted for 14.2% (171 thousand metric tons) of the total volume and 22.3% ($628 M) of the value of aquatic food production (DFO 2006) indicating the importance of this sector for food production. World trends continue to forecast growth of the aquaculture industry, with a focus on finfish, at rates greater than for other food-production sectors. In Canada the majority of cultured fisheries production arises from salmon farming on both coasts and in inland facilities, and from hatchery programs on the Pacific coast.

HISTORY OF WILD AND CULTURED SALMONID INTERACTIONS

Salmon culture began in Europe in the last millennium and in North America in the middle of the 17th century, but intensive application of salmonid enhancement and aquaculture only began in the 1960s. Since then, production of salmonids has expanded dramatically in many countries in North America, Europe, Australasia, and South America, providing significant economic benefit to those regions. A large portion of salmon culture is conducted in net pens in marine environments, but cultured fish are also reared in hatcheries.

Cultured fish may enter the natural environment by purposeful release for conservation and enhancement purposes, or they may escape from aquaculture facilities. Over the past 20 years, fisheries biologists have noticed that escaped farmed salmon were present in wild populations (Carr et al. 1997a; Clifford et al. 1998; Crozier 1993; Gudjonsson 1991; Hansen et al. 1987; Jacobsen et al. 1992; Lura and Sægrov 1991; McKinnell et al. 1997; Morton and Volpe 2002; Volpe et al. 2000). Concern has emerged regarding the concurrent genetic and ecological consequences of this interaction arising from differences in phenotype and genotype between cultured and wild fish populations (Crossman 1991; Fleming et al. 1996; Hansen et al. 1997; Hindar et al. 1991). Early reviews of the literature on the outcome of interaction between introduced and native fish populations suggested that introductions have usually been harmful to the native fish populations (Allendorf 1991; Hindar et al. 1991), but see (Peterson 1999).

PHENOTYPIC CHARACTERISTICS OF CULTURED SALMON

SCOPE OF THE ISSUE

Domestication can have a significant influence on life history traits in salmonids (Thorpe 2004); see Table 1 for a summary of documented phenotypic differences between domestic and wild fish. Many fitness-related traits such as growth, competitive ability, and anti-predator behavior have been found to have a genetic component. Domestication may select for traits related to improved growth rates, earlier age at

maturity and spawning, greater survival, increased tolerance to high temperature, and resistance to disease (*Hynes* et al. *1981*). Differences between wild and cultured fish represent a continuum, ranging from differences among natural strains, to differences between wild and sea-ranched fish, to differences between wild and highly selected and domesticated cultured fish. Alterations in fitness-related traits in hatchery fish should be typical of differences expected in aquacultured salmon, although the latter may show a greater magnitude of change due to an increased length of time under intentional and indirect selection, which is usually conducted in isolation from wild genetic pools. Transgenic fish, which can be viewed as an extreme form of domestication, are not considered in the present discussion except when examined as a model system for assessment of genotype/phenotype relationships (Devlin et al. *2001*).

The phenotypic differences found between cultured and wild strains may not only be due to genetic differentiation between the strains. They may also occur as a consequence of the different environments in which the fish are reared. Few studies have definitively assessed the relative contribution of genotype and environment. This complicates efforts to find trends in the growing body of literature on phenotypic differences between wild and farmed salmonids. Additionally, even when it is known that a trait is due to genetic differentiation between the strains, there is still a lack of knowledge regarding the expression of the different genotypes in different environments (i.e. genotype by environment interaction).

Table 1. Summary of phenotypic differences between cultured and wild fish.

TRAIT	RESULT	ENVIRONMENT	E	G	SPECIES	SOURCE
Morphology	Altered	Culture	+	+	Atlantic salmon	Fleming & Einum 1997
	Altered	Culture	+	0	Atlantic salmon	Fleming et al. 1994
	Altered	Wild	+	+	Coho salmon	Swain et al. 1991
Growth	Increased	Wild	+	+	Rainbow trout	Ayles 1975
	Increased	Wild	+	+	Rainbow trout	Ayles & Baker 1983
	Increased	Culture Wild	0	+	Atlantic salmon	Einum & Fleming 1997
	Increased	Culture	0	+	Atlantic salmon	Fleming & Einum 1997
	Decreased	Semi-Natural	0	+	Atlantic salmon	Fleming & Einum 1997
	Increased	Wild	0	+	Atlantic salmon	Fleming et al. 2000
	Increased	Culture	0	+	Atlantic salmon	Fleming et al. 2002
	Increased	Culture	0	+	Brook trout	Flick & Webster 1964
	No difference	Semi-Natural	0	-	Brook trout	Flick & Webster 1964
	Increased	Culture	0	+	Coho salmon	Hershberger et al. 1990
	Decreased	Wild	+	+	Brook trout	Keller & Plosila 1981
	Increased	Wild	+	+	Brook trout	Lachance & Magnan 1990
	Increased	Culture	+	+	Brook trout	Mason et al. 1967
	Decreased	Wild	+	+	Brook trout	Mason et al. 1967
	Increased	Culture	0	+	Coho salmon	McClelland et al. 2005
	Increased	Wild	0	+	Atlantic salmon	McGinnity et al. 1997
	Increased	Wild	0	+	Atlantic salmon	McGinnity et al. 2003
	Increased	Culture	0	+	Rainbow trout	Tymchuk & Devlin 2005
	Increased	Culture	0	+	Coho salmon	Tymchuk et al. in press
	Increased	Semi-natural	0	+	Coho salmon	Tymchuk et al. in press
Metabolism & Physiology	Altered	Culture	+	+	Brown trout Rainbow trout	Carline & Machung 2001

	No difference	Culture	0	-	Atlantic salmon	Dunmall & Schreer 2003
	Altered	Culture	0	+	Atlantic salmon	Fleming et al. 2002
	Altered	Culture	0	+	Atlantic salmon	Handeland et al. 2003
	Altered	Culture	+	+	Atlantic salmon	Poppe et al. 2003
	Altered	Culture	+	+	Atlantic salmon	Poppe et al. 1997
	No difference	Culture	0	-	Brown trout	Sanchez et al. 2001
	Altered	Culture	0	+	Atlantic salmon	Thodesen et al. 1999
Aggression	Increased	Culture	0	+	Atlantic salmon	Einum & Fleming 1997
	Increased	Culture	0	+	Atlantic salmon	Fleming & Einum 1997
	Decreased	Semi-natural	0	+	Atlantic salmon	Fleming & Einum 1997
	Increased	Wild	0	+	Atlantic salmon	McGinnity et al. 2003
	Increased	Wild	0	+	Atlantic salmon	McGinnity et al. 1997
	No difference	Culture Heterogenous substrate	+	-	Atlantic salmon	Mork et al. 1999
	Decreased	Culture Homogenous substrate	+	+	Atlantic salmon	Mork et al. 1999
Anti-predator behavior	Decreased	Culture	0	+	Atlantic salmon	Einum & Fleming 1997
	Decreased	Culture	0	+	Atlantic salmon	Fleming & Einum 1997
	No difference	Semi-natural	0	-	Atlantic salmon	Fleming & Einum 1997
	Decreased	Culture	0	+	Steelhead trout	Johnsson & Abrahams 1991
	Decreased	Culture	0	+	Atlantic salmon	Johnsson et al. 2001
	Decreased	Culture	0	+	Coho salmon	Tymchuk et al. in press
Foraging behavior	No difference	Wild	-	-	Atlantic salmon	Jacobsen & Hansen 2001
Habitat selection & Dispersal	No difference	Wild	0	-	Atlantic salmon	Einum & Fleming 1997
	Altered	Culture	+	+	Atlantic salmon	Mork et al. 1999
	Altered	Semi-natural	+	+	Masu salmon	Nagata et al. 1994
Survival	Decreased	Wild	+	+	Brown trout	Aerestrup et al. 2000
	No difference	Wild	0	-	Atlantic salmon	Einum & Fleming 1997
	Decreased	Wild, summer	0	+	Brook trout	Flick & Webster 1964
	No difference	Wild, winter	0	-	Brook trout	Flick & Webster 1964
	Variable	Wild	+	+	Brook trout	Fraser 1981
	Decreased	Wild	+	+	Brook trout	Keller & Plosila 1981
	Decreased	Wild	+	+	Brook trout	Lachance & Magnan 1990
	Increased	Wild, winter	+	+	Brook trout	Mason et al. 1967
	Decreased	Wild, summer	+	+	Brook trout	Mason et al. 1967
	Decreased	Wild	0	+	Atlantic salmon	McGinnity et al. 2003
	Decreased	Wild	0	+	Atlantic salmon	McGinnity et al. 1997
Migration	Altered	Wild	+	+	Atlantic salmon	Heggberget et al. 1993
	Altered	Wild	+	+	Atlantic salmon	Webb et al. 1991

Reproductive Physiology	Altered	Wild	+ +	Brook trout	Lachance & Magnan 1990
	No difference	Culture	0 -	Chinook salmon	Bryden et al. 2004
Spawning behaviour	Altered	Wild	0 +	Atlantic salmon	Fleming et al. 2000
	Altered	Semi-natural	+ +	Atlantic salmon	Fleming et al. 1996
	Altered	Wild	+ +	Atlantic salmon	Lura et al. 1993
	Altered	Wild	+ +	Atlantic salmon	Okland et al. 1995
	Altered	Wild	+ +	Atlantic salmon	Sægrov et al. 1997
	Altered	Semi-natural	0 +	Atlantic salmon	Weir et al. 2005
Reproductive success	Decreased	Wild High density	+ +	Atlantic salmon	Clifford et al. 1998
	Increased	Wild Low density	+ +	Atlantic salmon	Clifford et al. 1998
	Decreased	Wild	0 +	Atlantic salmon	Fleming et al. 2000
	Decreased	Semi-natural	+ +	Atlantic salmon	Fleming et al. 1996
	Decreased	Wild High density	+ +	Atlantic salmon	Sægrov et al. 1997
	No difference	Wild Low density	- -	Atlantic salmon	Sægrov et al. 1997
	Decreased	Semi-natural	+ +	Atlantic salmon	Weir et al. 2004

The result is the observed characteristic of the farmed fish in relation to the wild fish. The cause is due to environment (E) or genotype (G) and was either found to exist (+), not exist (-) or was not tested (0). An environmental cause for phenotypic differences refers to the environment experienced by the fish prior to the experiment. A positive contribution for both E and G indicates either that the experimental design could not isolate the contribution of one factor, or that both factors affected phenotype.

MORPHOLOGICAL AND BIOCHEMICAL DIFFERENCES

Morphological differences between cultured and wild salmon have been reported (Table 2) but in most cases, environment rather than genetics was found to have the most influence on these characteristics (Fleming et al. 1994; Kazakov and Semenova 1986; Swain et al. 1991). Fleming et al. (1994) and Einum and Fleming (2001) have noted that some morphological features associated with juvenile hatchery fish persist into the marine phase, whereas others do not. Fleming and Einum (1997) did find morphological differences between farmed and wild Atlantic salmon (farmed individuals had a more robust body and smaller rayed fins) that were caused by genetic differences since all fish were reared in the same environment for the experiment (common-garden experiment).

Table 2. Morphological differences between cultured and wild salmonids.

SPECIES	RESULT	SOURCE
Atlantic salmon	F more robust with smaller rayed fins relative to W	Fleming & Einum 1997
	F had smaller heads and fins and narrower caudal peduncles; F were more robust with smaller rayed fins	Fleming et al. 1994

F = farmed, D = domestic, Hy = hybrid, W = wild

Thus, rearing fish in a culture environment can lead to environmentally determined differences in morphology relative to fish reared in the wild. The extent of these differences will depend on the length of time spent within the artificial environment, and the intensity of the culture conditions (such as crowding, food supply, etc.). Multiple generations of strains kept within the culture environment could lead to genetically based morphological differences arising from selection for traits affording fitness benefits in culture.

EMERGENCE TIMING AND EMBRYONIC GROWTH

There are few studies on the genetic basis of differences in development rate between cultured and wild fish (Table 3). Differences in development rate have been noted between hatchery and wild strains of rainbow trout (Ferguson et al. 1985) and it has been determined that development rate is controlled by at least one major locus in this species (Robison et al. 2001; Robison et al. 1999). The actual genes affecting this process in domesticated fish are not yet known, although the expression of growth hormone genes in transgenic fish has been shown to significantly affect development rate with consequent effects on survival fitness (Devlin et al. 2004; Sundström et al. 2005).

Table 3. Differences in development between cultured and wild salmonids.

SPECIES	RESULT	SOURCE
Rainbow trout	Controlled by at least one major locus	Robison et al. 199, 2001

We need to increase our understanding of the influence of domestication on embryonic development rates because timing of emergence of fry from redds can have a significant effect on fry survival (through altered predation risk or competition advantage) and is often adapted for the local environment.

GROWTH

Fast-growing strains of commercially important salmonids have been developed through the use of selective breeding programs (Gjedrem 1983; Gjerde 1986; Hershberger et al. 1990). Both mass and family selection methods have been utilized, with the typical levels of growth enhancement achieved being approximately 10–15% per generation. Heritabilities for growth enhancement remain relatively high (> 0.2), indicating that sufficient genetic variability remains within many aquacultured strains to allow for further enhancement of this trait (Gjedrem 2000). In general, domestic fish tend to grow faster than wild fish, although this is not universally the case (Bryden et al. 2004; Einum and Fleming 2001). Growth is greatly influenced by the rearing environment (Table 4). The following sections summarize growth enhancements which have been achieved by domestication among different salmonid species.

Table 4. Differences in growth between cultured and wild salmonids.

SPECIES	RESULT	SOURCE
Atlantic salmon	F had higher growth rate in the hatchery and wild	Einum & Fleming 1997
	F outgrew W in the hatchery, W outgrew F in a semi-natural habitat	Fleming & Einum 1997
	Hy outgrew W in the natural environment	Fleming et al. 2000
	F outgrew W	Fleming et al. 2002
	F outgrew W	McGinnity et al. 1997, 2003, 1997
Brook trout	D maintained size advantage relative to W when released into semi-natural ponds and allowed to over-winter	Flick & Webster 1964
	F had lower growth relative to W in the wild	Keller & Plosila 1981
	D grew faster than Hy and W in hatchery but could not maintain this growth advantage in the wild	Mason et al. 1967
	D and Hy maintained size advantage over W when released into small lakes (over two year period)	Lachance & Magnan 1990
Pacific salmon and trout	F outgrew W	Ayles et al. 1979; Ayles & Baker 1983
	F outgrew W	Lachance & Magnan 1990
	F demonstrated 60% increase in weight	Hershberger et al. 1990
	F outgrew W	McClelland et al. 2005
	F outgrew W	Tymchuk et al. in press; Tymchuk & Devlin 2005

F = farmed, D = domestic, Hy = hybrid, W = wild

Atlantic salmon and sea trout

Altered selection has been observed to cause genetic changes leading to faster growth of farmed Atlantic salmon (Fleming et al. 2000, 2002; Fleming and Einum 1997; Gjedrem 1979; Johnsson et al. 1996; Kallio-Nyberg and Koljonen 1997; McGinnity et al. 1997, 2003; McGinnity et al. 1997; Petersson and Järvi 1995). An additional study found that farmed strains of both Atlantic salmon and sea trout were larger at smolt, but the study could not differentiate between environmental or genetic influence (Petersson et al. 1996).

Brook trout

Domestic brook trout (propagated for >30 years) have been observed to grow faster than both wild and hybrid fish in the hatchery, but were not able to maintain their growth advantage in the wild (Mason et al. 1967). Other studies found that faster-growing

domestic strains of brook trout were able to maintain their growth advantage relative to wild strains when reared in semi-natural ponds (Flick and Webster 1976; Lachance and Magnan 1990).

Pacific salmon and trout

Farmed strains of coho salmon can grow faster than non-selected native strains (Devlin et al. 2001; McClelland et al. 2005; Tymchuk et al. in press). Differentiation in growth rate in domestic compared with wild strains can occur in a relatively short period of time as coho salmon have demonstrated a 60% increase in mass after only four generations under a selective breeding program (Hallerman and Kapuscinski 1992). Domestic rainbow trout have been shown to grow much faster than wild rainbow trout strains (Devlin et al. 2001; Tymchuk and Devlin 2005) and are able to maintain their growth advantage when reared in natural lakes (Ayles and Baker 1983; Flick and Webster 1976; Lachance and Magnan 1990).

General trends in growth

Environmental factors such as availability of food resources and temperature will, of course, have an influence on growth of fish. However, there can also be large differences in growth between cultured and wild strains that are due to genetic differences between the strains. The magnitude of the growth differences caused by genotype will be dependent on the purpose and history of the cultured strain. Aquacultured strains that have been intensely selected for enhanced growth will show a larger shift in growth phenotype from the founding line relative to a strain that has not experienced directed selection. There is still limited knowledge on how environment will act on the inherent genetic differences (i.e. will environmental conditions affect different genotypes in distinct ways through genotype x environment interactions?).

METABOLISM AND PHYSIOLOGY

There is limited information on the physiological differences between farmed and wild strains (Table 5). It is often thought that altered feed conversion efficiency underlies the ability of farmed strains of fish to growth faster. This has been supported by studies on Atlantic salmon (Thodesen et al. 1999) although no differences in conversion efficiency were found between wild and selected strains of brown trout (Sanchez et al. 2001). Altered endocrine regulation, particularly that involving changes of the growth hormone / insulin-like growth factor axis, may also explain the enhanced growth of selected strains of fish (Fleming et al. 2002).

Selection in a culture environment may also alter smolting physiology. Atlantic salmon reared in the hatchery had altered timing of metabolic changes for smolting relative to wild fish (Leonard and McCormick 2001), and smolts from wild strains were better able to tolerate transfer to seawater (Handeland et al. 2003). Wild fish were found to have an increased tolerance to saltwater relative to hatchery conspecifics (Shrimpton et al. 1994), although these differences may be due to rearing environment. Ugedal et al. (1998) found that both wild and hatchery fish migrating downstream had well -developed seawater tolerance. Upon release, hatchery honmasu parr had elevated levels of growth hormone while those of wild parr did not increase.

Additional differences detected between farmed and wild fish that may lead to physiological differences include altered swimbladder (Poppe et al. 1997) in farmed Atlantic salmon and altered heart morphology in both Atlantic salmon and rainbow trout (Poppe et al. 2003). It is suggested that the observed differences may lead to a decrease tolerance of stress in the farmed fish. Domestic strains of rainbow and brown trout were found to have altered critical thermal maxima relative to wild strains (Carline and Machung 2001). These differences were suggested to be genetically determined.

Physiology may not always differ between farmed and wild strains. For example, no differences in swimming and cardiac performance were observed between farmed and wild Atlantic salmon (Dunmall and Schreer 2003).

Table 5. Differences in metabolism and physiology between cultured and wild salmonids

SPECIES	RESULT	SOURCE
Rainbow trout and brook trout	Altered critical thermal maxima	Carline et al. 2001
Atlantic salmon	No differences in swimming and cardiac performance	Dunmall and Schreer 2003
Atlantic salmon	F had higher levels of pituitary growth hormone	Fleming et al. 2002
Atlantic salmon	W smolts had better tolerance of seawater	Handeland et al. 2003
Atlantic salmon and rainbow trout	Altered heart morphology	Poppe et al. 2003
Atlantic salmon	Altered swimbladder	Poppe et al. 1997
Brown trout	No differences in feed conversion efficiency	Sanchez et al. 2001
Atlantic salmon	F had higher feed conversion efficiency	Thodesen et al. 1999

F = farmed, D = domestic, Hy = hybrid, W = wild

In general, cultured fish will tend to show physiological differences relative to wild fish. However, it is often not clear whether these differences are a cause or a consequence of other phenotypic differences such as growth or behavior between the strains. It is therefore difficult to clarify whether physiological differences have a genetic basis per se, or if they are a product of the environment. Any observed differences are likely due to a combination of these factors, unless cultured strains have been specifically selected for altered physiological characteristics such as higher feed conversion efficiencies.

AGGRESSIVE BEHAVIOR

Aggressive behavior is often affected by artificial rearing (Table 6). A study on the agonistic behavior of domestic and wild steelhead trout suggested that four to seven

generations of domestication resulted in behavioral divergence of the two populations (Berejikian et al. 1996), although Johnsson et al. (1996) found no difference in dominance between fish selected for enhanced growth and wild individuals. Studies on domestic farmed Atlantic salmon found genetically based increases in aggression level relative to wild fish (Einum and Fleming 1997; Fleming et al. 2002; McGinnity et al. 1997, 2003). In one study examining brown trout, hatchery-reared fish of hatchery genotype were more aggressive than hatchery-reared fish of wild genotype introduced into a stream at the same time, but less aggressive than resident wild fish. Concurrently, the hatchery-reared fish had a lower rate of growth relative to both the resident and introduced wild fish (Deverill et al. 1999). In contrast, hatchery coho salmon parr dominated wild parr even though the wild parr had a prior resident advantage (Rhodes and Quinn 1998). Similar results were obtained by (Swain and Riddell 1990) where hatchery juvenile coho salmon were more aggressive than wild fish and in this case, experimental design revealed that differences were caused by genetic rather than environmental effects.

Interestingly, other research has found that selection for enhanced growth results in indirect selection for tameness, as opposed to aggression (Doyle and Talbot 1986). For example, wild Atlantic salmon were found to make more aggressive attacks toward farmed individuals than farmed made on wild (Mork et al. 1999). In an attempt to explain the discrepancy relating to the genetic link between aggressive behavior and growth, (Ruzzante and Doyle 1991) concluded that agonistic behavior will be inversely proportional to growth when selection occurs in an environment with forced social interaction and unlimited food resources.

Table 6. Differences in aggression between cultured and wild salmonids.

SPECIES	RESULT	SOURCE
Atlantic salmon	F more aggressive	Einum & Fleming 1997
Atlantic salmon	F dominated W in tank, W dominated F in semi-natural habitat	Fleming & Einum 1997
Atlantic salmon	F competitively displaces W downsteam	McGinnity et al. 1997
Atlantic salmon	W displayed higher levels of agonistic behaviour relative to F	Mork et al. 1999

F = farmed, D = domestic, Hy = hybrid, W = wild

Cultured and wild fish do show differences in their levels of aggression towards conspecifics, although there has not been a consistent trend as to whether aggression increases or decreases under culture. The common assertion is that aggression will decrease under culture when fish are reared in crowded conditions and do not have to fight for limited food resources. Knowledge is lacking on the expression of genetically determined differences in aggression under varied environmental conditions and the extent of behavioral plasticity that can be expressed by the different strains.

PREDATION RISK

Several studies indicate that anti-predator behavior has been altered through domestication so that domesticated fish are more willing to risk predation to feed and consequently may have higher mortality rates (Table 7). Farmed Atlantic salmon show increased risk-taking behavior relative to wild fish (Einum and Fleming 1997; Fleming et al. 2002; Fleming and Einum 1997) and a reduced response to predators, as measured by flight and heart rate response (Johnsson et al. 2001). Juvenile farmed coho salmon begin feeding sooner after a simulated predator attack relative to wild coho (Tymchuk et al. 2006) and domestic/wild hybrid rainbow trout with enhanced growth rate have been observed to be more willing to risk predation to feed relative to wild individuals (Johnsson and Abrahams 1991). Similarly, brown trout selected for enhanced growth showed reduced anti-predator behavior relative to wild fish (Johnsson et al. 1996), and growth-enhanced transgenic salmonids have been observed in some, but not all, cases to expose themselves to greater predation risk and suffer higher levels of predation mortality (Abrahams and Sutterlin 1999; Sundström et al. 2003, 2004, and 2005; Vandersteen Tymchuk et al. 2005).

Table 7. Differences in predation risk between cultured and wild salmonids.

SPECIES	RESULT	SOURCE
Atlantic salmon	F and Hy less responsive to predation risk	Einum & Fleming 1997
Atlantic salmon	F less responsive to predation risk	Fleming & Einum 1997
Atlantic salmon	D less responsive to predation risk	Johnsson et al. 2001
Brown trout	F less responsive to predation risk	Johnsson et al. 1996
Steelhead trout	Hy less responsive to predation risk	Johnsson & Abrahams 1991
Coho salmon	F less responsive to predation risk	Tymchuk et al. in press

F = farmed, D = domestic, Hy = hybrid, W = wild

A genetically determined reduced response to predators seems to be a consistent trend in domestic strains across several species. However, these studies have tested the predator response in an artificial environment with no real risk of being consumed by a predator. Few studies directly test whether the domestic strains would respond to a real predator in the wild or, more importantly, to overall fitness if their realized mortality would be any different from that experienced by the wild fish.

FORAGING BEHAVIOR

Currently, there are few studies on foraging behavior directed specifically at farmed fish (Table 8), so the following examples include studies on hatchery fish. In

addition to being more willing to risk predation to feed, domestic fish may have altered foraging strategies relative to wild individuals. These foraging strategies may not be as suitable for the natural environment as they have evolved within the structure of the culture environment. Hatchery reared brown trout have been observed to feed less and move more, generating more foraging costs overall relative to wild brown trout in the same stream (Bachman 1984). Bachman (1984) postulated that high-energy costs are a prominent cause for high mortality of released fish into the wild. Hatchery-reared brown trout demonstrated less effective foraging ability initially after release from culture, but showed a rapid learning curve when subsequently foraging for wild prey. After approximately one week, they were feeding nearly as well as the wild fish. This effect was most apparent in May when food sources were plentiful; there was greater discrepancy between hatchery and wild foraging consumption during periods when food was low (Johnsen and Ugedal 1986). Hatchery honmasu salmon released into the wild began feeding immediately on natural prey, however their stomach fullness was lower than that of wild fish for one week after release (Munakata et al. 2000). Stomach analysis of escaped farmed Atlantic salmon in the Pacific indicates that these fish are capable of successful feeding (McKinnell et al. 1997). Escaped farm Atlantic salmon off the Faroe Islands show feeding patterns typical of wild fish (Jacobsen and Hansen 2001).

Table 8. Differences in foraging behaviour between cultured and wild salmonids.

SPECIES	RESULT	SOURCE
Atlantic salmon	No differences in diet	Einum & Fleming 1997
Atlantic salmon	No difference in feeding pattern of escaped and wild fish	Jacobsen & Hansen 2001

F = farmed, D = domestic, Hy = hybrid, W = wild

There is no evidence for a strong genetic basis for any observed differences in foraging strategy. Environment would likely have a strong effect on this phenotypic characteristic, and in nature would be expected to quickly overcome any genetic differences that had evolved within a culture environment (since if an individual did not eat, it would die). A genetic basis for this trait would probably be due to phenotypic expression of other phenotypic traits such as growth or morphology that would drive foraging behavior characteristics.

HABITAT SELECTION AND DISPERSAL

Differences in habitat selection (Table 9) may reduce the potential for interaction between wild and cultured fish, or limit the ability of escaped fish to successfully locate and acquire food resources to meet their metabolic requirements. Hatchery cutthroat trout spent a greater proportion of time in riffles relative to wild fish and were more aggressive (Mesa 1991). This elevated expenditure of energy (unnecessary aggression and use of fast-flowing water) may be expected to limit the ability of domestic fish to survive in the wild. Fifth-generation farmed Atlantic salmon have been found to spend more time

feeding pelagically and used more of the water column than did wild fish, who spent more time hiding (Mork et al. 1999). Similarly, hatchery-reared Atlantic salmon were found to maintain a higher position within the water column relative to wild individuals (Dickson and MacCrimmon 1982).

Dispersal clearly plays an important role in determining the fitness of salmon in nature, and differences in this trait (Table 9) have been found between hatchery and wild salmonids. Domestic masu salmon released as unfed alevins and eyed eggs tended to disperse upstream, while wild fish tended to disperse downstream and also tended to disperse more extensively than domestic fish (Nagata et al. 1994). Hatchery-reared trout had lower dispersal and upstream movement relative to concurrently stocked wild fish (Jørgensen and Berg 1991). Differences have also been observed in the use of a river estuary by hatchery and wild chinook salmon (Levings et al. 1986), with hatchery fish spending approximately half the amount of time in the estuary as did wild.

Table 9. Habitat selection and dispersal differences between cultured and wild salmonids.

TRAIT	RESULT	SPECIES	SOURCE
Habitat selection	No differences in current or depth occupied by F and W	Atlantic salmon	Einum & Fleming 1997
	F spent more time feeding pelagically and used more of the water column	Atlantic salmon	Mork et al. 1999
Dispersal	D fish tended to disperse upstream and less extensively than W fish, that tended to disperse downstream	Masu salmon	Nagata et al. 1994

F = farmed, D = domestic, Hy = hybrid, W = wild

As with foraging behavior, there are limited data on which to make conclusions regarding any genetically based differences in habitat selection and dispersal between cultured and wild fish. Although the method of feeding within the culture environment may alter use of habit, differences observed for this trait could also be due to underlying physiological differences and not direct selection on the trait itself.

SURVIVAL

Escaped domesticated salmon can survive in the wild, although recapture rates of farmed fish vary considerably (Table 10). The ability of farmed fish to survive upon escape and successfully mature will depend on several factors including the timing of escape and whether the escape location is adjacent to spawning streams (Hansen and Jonsson 1994). The recapture rate of wild Atlantic salmon (2.3%) in the Faroese fishery was significantly higher than the recapture rate of escaped farmed fish at 1.2% (Hansen et al. 1997). Survival of farmed, wild, and hybrid Atlantic salmon parr was similar after release to a stream (Einum and Fleming 1997), but progeny of naturally spawned farmed Atlantic salmon had reduced survival (McGinnity et al. 2003; McGinnity et al. 1997). Recapture rates of domestic, hybrid, and wild brook trout planted in seven lakes were similar in three lakes, while in another four lakes, domestic fish had lower recapture rates

than the hybrid and wild fish (Fraser 1981). Hybrid fingerling brook trout had better survival than wild and domestic fish released into a pond (Keller and Plosila 1981). Domestic brook trout had better over-winter survival, but experienced higher mortality during the summer fishing season relative to wild fish (Flick and Webster 1964; Mason et al. 1967).

Similar trends in survival have been indicated by studies on hatchery fish. Wild steelhead trout had the highest rate of survival in a stream environment (Reisenbichler and McIntyre 1977). This was in contrast to a hatchery environment, where hatchery fish had the highest survival. Survival of wild brown trout populations was three times that of hybrid or hatchery fish (Skaala et al. 1996) and similar results were found when comparing hatchery-reared and native trout (Weiss and Schmutz 1999). Wild brown trout smolts had higher survival rates relative to domesticated smolts (Aarestrup et al. 2000), even though they were smaller when released into a river from the hatchery. Returns of stocked Scottish salmon were significantly lower than the returns of the wild fish (Verspoor and De Leaniz 1997).

Importantly, not all studies have indicated that domesticated fish will incur higher mortality rates in nature. Hatchery-reared Atlantic salmon smolts did not suffer increased mortality relative to wild smolts in an estuary of the River Orkla in Norway (Hvidsten and Lund 1988). Such effects may depend highly on specific environmental conditions. For example, upstream from a hatchery, cormorants were found to consume only wild salmonids, while downstream predation was restricted to hatchery-reared fish (Kennedy and Greer 1988).

Table 10. Differences in survival.

SPECIES	RESULT	SOURCE
Brown trout	Survival better for W than D	Aerestrup et al. 2000
Atlantic salmon	Survival similar for F, Hy and W	Einum & Fleming 1997
Brook trout	D fish had lower over-summer survival relative to W, no difference in over-winter survival	Flick & Webster 1964
Brook trout	D, Hy, and W had similar survival in three lakes; D had lower survival than Hy and W in four lakes	Fraser 1981
Brook trout	Hy had better survival than D or W fingerlings stocked into a pond	Keller & Plosila 1981
Brook trout	D had lower survival than W when released into lakes, with Hy having intermediate survival	Lachance & Magnan 1990
Brook trout	Survival of D higher over winter, W better over summer when fishing was open	Mason et al. 1967
Atlantic salmon	Survival of F less than W	McGinnity et al. 1997, 2003

F = farmed, D = domestic, Hy = hybrid, W = wild

Survival is influenced by all other phenotypic traits and the environment in which they are expressed. Cultured fish, either through a plastic response to their environment or through an adaptive response to altered selection pressures, tend to express phenotypic characteristics best suited for the culture environment. Consequently, they tend to not have as high survival as wild fish in a natural environment. However, it is still not clear whether cultured fish that experience a natural environment throughout their life history will still show decreased survival relative to the wild fish. It is not known how strong the genetic basis of survival is, or whether the cultured fish still have the ability to show a phenotypically plastic response to the environment that will maximize their ability to survive.

SEXUAL MATURATION AND SPAWNING

Genetic effects of farmed fish on wild populations will depend in part on the reproductive behavior of farmed fish in the wild. Evidence suggests that farmed fish have the ability to breed successfully in the wild, although contradicting results do occur. There are generally significant differences in breeding potential (Table 11) of cultured and wild fish (Fleming and Gross 1992, 1993; Fleming et al. 1996), although other studies have found similar reproductive success for hatchery and native fish in the wild (Dannewitz et al. 2004; Palm et al. 2003). Morphology and life history traits related to reproductive behavior respond evolutionarily to altered selection regime in the hatchery environment (Fleming 1994; Fleming and Gross 1989). The genetic effects of aquacultured salmon on wild populations will depend not only on the size of the wild population, but also on variation in breeding success (Fleming and Petersson 2001). The following sections describe aspects of reproductive success in cultured and wild salmonids.

Table 11. Differences in reproductive behaviour and success between cultured and wild salmonids.

TRAIT	RESULT	SPECIES	SOURCE
Maturation and migration	F adults migrated to nearby streams in a random manner	Atlantic salmon	Heggberget et al. 1993
	F adults did not migrate as far up the river	Atlantic salmon	Webb et al. 1991
Reproductive physiology	D had higher gonadosomatic index relative to W and Hy	Brook trout	Lachance & Magnan 1990
	No difference in fecundity between F and W	Chinook salmon	Bryden et al. 2004
Spawning behaviour	F spawned earlier	Atlantic salmon	Fleming et al. 2000
	F males were less aggressive, courted less, and participated in fewer spawnings relative to W	Atlantic salmon	Fleming et al. 1996

	F redds had a greater number of egg pockets with fewer eggs per pocked relative to W	Atlantic salmon	Lura et al. 1993
	F females moved more and F fish spent less time in spawning area	Atlantic salmon	Okland et al. 1995
	F spawned earlier	Atlantic salmon	Sægrov et al. 1997
	F and W parr may or may not show differences in aggression	Atlantic salmon	Weir et al. 2005
Reproduction	At high density, F had reduced success relative to W; at low density, there was no difference in success	Atlantic salmon	Clifford et al. 1998a,b
	25-35% of eggs in river of F origin	Atlantic salmon	Carr et al. 1997
	Lifetime reproductive success of F less than W	Atlantic salmon	Fleming et al. 2000
	Lifetime reproductive success of F less than W	Atlantic salmon	Fleming et al. 1996
	W fish had higher reproductive success than F at high densities, no difference at low densities	Atlantic salmon	Sægrov et al. 1997
	F males had reduced spawning success relative to W males	Atlantic salmon	Weir et al. 2004
	escaped F females hybrized more frequently with trout than W	Atlantic salmon	Youngson et al. 1993

F = farmed, D = domestic, Hy = hybrid, W = wild

Age of maturation and spawning migration

Migration and maturation timing have demonstrated high heritabilities and genetic correlation for populations of chinook salmon, indicating that these traits would respond rapidly to selection and may accelerate selection for other traits by producing reproductively isolated populations (Quinn et al. 2000). The breeding system of Atlantic salmon evolves through selection on viability and sexual selection for breeding opportunities. Introduced salmon alter the frequency of different breeding phenotypes (due to differences in morphology), which will alter selection and thereby influence the breeding system (Fleming 1998). Although this is not a direct genetic affect, over time the altered selection parameters may cause a concurrent change in the genetic profile that defines the breeding strategy.

Hatchery-reared Atlantic salmon can have altered age at maturity relative to wild fish, with the hatchery fish producing a higher proportion of mature grilse (Kallio-Nyberg and Koljonen 1997) due in part to the elevated growth rates induced by food availability in the hatchery. Comparisons of hatchery and wild summer and winter steelhead trout indicated that hatchery fish returned earlier than wild in both the summer and winter returns (Leider et al. 1986), and further, the hatchery fish had a lower number of saltwater age categories relative to the wild fish. Hatchery and wild summer steelhead were found

to be more similar than hatchery and wild winter steelhead, indicating that the life history strategies of the local populations must be considered when assessing differences, and potential interaction, between domesticated and wild fish.

To reproduce successfully, farmed salmon must be capable of finding suitable spawning areas in streams. The farmed salmon may have more difficulty in homing to appropriate spawning streams, as they may not have been imprinted on the local freshwater streams (Hansen et al. 1987). One study found that farmed Atlantic salmon did migrate to nearby streams, albeit in a random manner (Heggberget et al. 1993), while the wild salmon released concurrently homed to the appropriate river more precisely and in a shorter period of time. Consquently, the largest salmon streams may receive the highest numbers of escaped farmed salmon, which are also the most important salmon streams in terms of potential for reproduction.

A study examining the spawning behavior of escaped sub-adult farmed Atlantic salmon in Scotland using radio tagging and direct observation revealed that farmed salmon tend to spawn later in the year and do not migrate as far upstream as do wild fish. It is possible that the lower migration of the farmed salmon occurred because some were raised in the hatchery, which is located in the lower reaches of the river to which they would have imprinted on (Webb et al. 1991). Delayed spawning may arise due to differences in genetic origin of the farmed and wild fish, since different stocks of Atlantic salmon are known to have divergent average spawning dates. Thus, genetic introgression of farmed genotypes into wild population may affect a specific demographic subset of a population preferentially.

Maturation morphology

Secondary sexual characteristics are reduced in cultured males relative to wild males (Hard et al. 2000) but the extent of genetic or environmental influence on these observations is unclear. The morphology of fish at maturity can be strongly influenced by environment (Bessey et al. 2004) making tests of genetic divergence of this trait difficult, particularly when the strains cannot be reared in a natural environment.

Reproductive physiology

Variation in egg mass and fecundity in brown trout is, in part, genetically determined (Jonsson and Jonsson 1999) and investment by hatchery fish was found to be greater than wild strains. Similarly, domestic fish from a lake had a higher gonadosomatic index relative to hybrid and wild brook trout, and concurrently higher fecundity (Lachance and Magnan 1990). Again, this is not universally observed since the fecundity of lake trout was not found to differ between hatchery and wild strains (Peck 1988), nor were differences observed between farmed and wild strains of chinook salmon (Bryden et al. 2004).

Spawning behavior

One study found that escaped farmed Atlantic salmon have reduced spawning success because farmed females moved more during spawning and the farmed fish spent less time in the spawning area relative to the wild fish (Okland et al. 1995). In a different study, escaped farmed female Atlantic salmon demonstrated differences in spawning behavior (redds of farmed fish contained more egg pockets and fewer eggs per pocket)

although all components of normal spawning behavior were present (Lura and Sægrov 1993). It seems that the most significant differences in spawning behavior may be exhibited by the males. Fleming et al. (1996) found farmed males to be less aggressive than wild males, with a consequent reduction in the number of females courted and in breeding success. Further studies indicated conflicting results when testing for differences in aggression between farmed and wild parr (Weir et al. 2004). The presence of differences among the strains of fish may be dependent on life-history stage in addition to genotype and environment.

Captively reared coho salmon of both sexes showed a full range of reproductive behavior demonstrated by wild fish (albeit reduced from normal levels). They also had the ability to spawn naturally in the wild (Berejikian et al. 1997; Bessey et al. 2004), although there may be a competitive advantage for wild females as they constructed more nests per individuals relative to the cultured females.

Reproductive success

Atlantic salmon: Some escaped farmed Atlantic salmon in NW Ireland were successful in completing their life cycle and breeding or interbreeding with wild fish (Clifford et al. 1997), although at an average success rate of only 7%, with a maximum breeding frequency of 70% in one river, (Clifford et al. 1998). At high densities, wild Atlantic salmon had better reproductive success than did escaped farmed fish, whereas there was no observed difference in reproductive success between farmed and wild fish when densities were low (presumably since mate choice was limited). In the River Vosso in Norway, escaped farmed fish were more prevalent (81%) and spawned earlier than wild fish and most fry in the river were of farmed origin. Using minisatellite DNA profiling, the reproductive success of secondary males (subdominant adults or parr, which mature in freshwater) was measured and compared for wild and sea-ranched Atlantic salmon (Thompson et al. 1998). Sea-ranched fish secondary males had higher reproductive success (48.2%) than wild secondary males (28.9%),

The Magaguadavic River located in the center of the New Brunswick salmon aquaculture industry has been monitored to study the effect of escaped farmed salmon entering the river. Over a period of four years, the numbers of wild fish decreased (to very low numbers of <10) while the numbers of escaped farmed fish increased. Analysis of the eggs indicated that 20% to 35% of the eggs were of farmed origin (Carr et al. 1997a). The farmed fish were found to enter the river later than the wild fish, and most of the farmed fish were sexually immature (Carr et al. 1997b). Examination of the gonadal tissue demonstrated that the farmed female salmon showed no sign of maturing upon the year of entry to freshwater, although some farmed males would be capable of interbreeding with wild females (Lacroix et al. 1997). Some fish may over-winter in the river and mature, thereby subsequently becoming capable of spawning.

After tracking the reproductive success of farmed and wild salmon released into a river, it was found that the farmed salmon, particularly the males, were reproductively inferior to the wild fish (Fleming et al. 1996, 2000). The overall reproductive success of the farmed fish was 16% of that of the wild fish in one study. However, the productivity of the native population was depressed by 30%, indicating resource competition and competitive displacement. Other results indicated that farmed females had less than one-third the reproductive success of wild females, with farmed males indicating only 1–3%

of the reproductive success of wild males (Fleming et al. 1996). These differences are usually due to inferior competitive ability on the spawning ground for the farmed males, and lower fecundity and inept egg care for the wild females. Hatchery experiments on farmed and wild fish support the observation that farmed males have reduced spawning success compared with wild males (Weir et al. 2004) However, not all adults in all experiments were derived from the same environment (wild or culture) so that effects likely are not due to genetic differences alone.

A different study demonstrated that farmed and hybrid Atlantic salmon parr reared in a near-natural environment had higher breeding and fertilization success than wild individuals (Garant et al. 2003). The authors suggest that introgression of domestic genes past the initial generation following sea-pen escape could be mediated by early maturing farm and hybrid males. Although initial gene flow is typically attributed to matings between wild males and domestic females, this trend may be reversed in consequent generations due to precocious parr. Discrepancies between the two previous studies are quite likely due to an environmental effect on the genetic differences between domestic and wild fish.

Brown trout: Studies with brown trout have shown that reproductive success may differ between male and female fish. Asymmetry between the male and female reproductive success was found by comparing measurements of inbreeding (as indicated by protein-coding loci and mitochondrial haplotypes) with the domestic females showing higher rates of introgression with the native fish (Poteaux et al. 1998b). Hatchery brown trout were found to interbreed with wild fish, with male hatchery fish contributing more to interbreeding than hatchery females (Hansen et al. 2000).

Pacific salmon: There is a lack of knowledge on the ability of farmed strains of Pacific salmon to spawn successfully in the wild. Some studies on hatchery strains of Pacific salmon may provide some indication of the expected results for farmed strains. There would likely be an even stronger effect of culture on their ability to reproduce successfully in the wild. Comparisons of spawning success of hatchery and wild coho salmon found trends similar to those observed for Atlantic salmon where the hatchery fish had reduced success (from both environmental and genetic causes), which was more severe in males (Berejikian et al. 1997, 2001; Fleming and Gross 1993; Fleming and Petersson 2001). Similarly, wild strains reared in culture conditions have reduced reproductive success (Berejikian et al. 1997; Bessey et al. 2004).

General conclusions

Consistent trends have been observed in that cultured fish often have the physiological ability to spawn, but altered spawning behavior can limit their success. Even though the reproductive success of farmed fish may be low, the potential for significant gene flow still exists since the population of farmed fish often outnumbers the population of resident wild fish (at least in the case for Atlantic salmon) at times by as much as 3:1 (Lund et al. 1994; Lura and Økland 1994). We do not have any data on the ability of farmed and wild Pacific salmon to spawn in nature, but comparisons between

hatchery and wild coho salmon indicate that trends observed for Atlantic salmon may be typical of the phenotypic changes expected during domestication.

WHY ARE CULTURED AND WILD FISH DIFFERENT?

GENOTYPE, ENVIRONMENT, AND GENOTYPE X ENVIRONMENTAL (G X E) INTERACTIONS

Phenotypic differences between farmed and wild salmonids may arise from a combination of genetic and environmental effects but the origin of the difference is not well defined in most cases. To assess genetic effects, experiments must be performed by rearing fish of different origins in a common environment. Environmental effects (i.e. phenotypic plasticity) can be tested by rearing fish of a common genetic background in different environments. As will be discussed below, cultured fish may have an altered genotype in response to selection pressures from an artificial environment, leading to genetically based phenotypic differences between the cultured and wild strains. Alternatively, since salmonids are so phenotypically plastic (Hutchings 2004), they may have an altered phenotype in response to the altered environmental conditions in which they are reared. These environmentally based phenotypic differences would not be passed along to offspring as they do not have a genetic basis. Thus, environmental effects are anticipated to have single generation effects arising directly from escaped fish, whereas genetic differences are those with the potential to affect a species on a longer time frame. The sensitivity of a phenotypic trait to environmental conditions (i.e. phenotypic plasticity) may itself have been altered through domestication. It is therefore critical to separate the influence of genotype and environment, and to understand genotype by environment interactions to fully predict the genetic effects of interaction between wild and cultured fish.

GENETIC MECHANISMS LEADING TO DIFFERENTIATION OF CULTURED AND WILD FISH

The mechanisms causing genetic changes in cultured fish include inbreeding, genetic drift and selection. Selection can be further broken down into three categories: artificial selection, domestication, and relaxation of natural selection. It is generally accepted that farming of salmon generates genetic change due to intentional and unintentional selection in culture (Fleming and Einum 1997; Reisenbichler and McIntyre 1977). In many cases, the goal of selection is to produce a homogeneous line that demonstrates constancy in the desirable traits such as enhanced growth (Gjedrem 2000). In cases here diversity is desired, domestication effects would be lower. Genetic changes may also occur for traits other than those that are the focus of the selective breeding program. For example, fifth-generation farmed Atlantic salmon differed significantly from wild populations in loci other than those chosen for the selective breeding program (Mjølnerød et al. 1997). The characteristic of the genetic changes caused by indirect selection during domestication can vary according to the method of fish culture and the extent of time that fish spend in the artificial environment (Utter and Epifanio 2002). For example, characteristics of the culture environment such as rearing density and the source

of food into the tank may affect the evolution of aggressive behavior or increased motivation for surface feeding.

DOCUMENTED CHANGES IN GENOTYPIC VARIABILITY OF CULTURED FISH

Differences are often found when comparing the genotype (of selectively neutral alleles) of cultured and wild fish (Table 12). A variety of methods have been used including, indirect methods (e.g. use of fluctuating asymmetry as a measure of genetic robustness and thus developmental stability), direct assessments of genetic variation (at the DNA level using single nucleotide polymorphisms detected by sequencing or restriction fragment polymorphism as well as micro- and minisatellite variation), or methods involving phenotypic assessments of progeny derived from genetic crosses.

Atlantic salmon

Artificially reared Atlantic salmon, selected for growth and disease resistance, were found to possess lower genetic variability as measured by mean heterozygosity and mean number of alleles at six enzyme loci (Cross and King 1983). It was argued that these genetic changes were caused by founder effects and genetic drift rather then selection. First-generation cultured Atlantic salmon had 26% less heterozygosity and 12% fewer alleles relative to wild fish, consistent with a loss of genetic variability expected from random drift, probably caused by using a small number of adults for the broodstock (Verspoor 1988). Other studies have further supported the trend that farmed Atlantic salmon typically have lower measures of genetic variability (14–45% reduction) relative to wild populations (Mjølnerød et al. 1997; Wilson et al. 1995). One study on the genetic variation between farmed and wild populations of Atlantic salmon found no significant difference in heterozygosity, but the farmed fish possessed lower total gene diversity (Danielsdottir et al. 1997). The genetic distance between the farmed population and the wild populations was as great as the genetic differences between separate wild populations.

Table 12. Differences in genetic variability between cultured and wild salmonids.

SPECIES	RESULT	SOURCE
Atlantic salmon	F had lower heterozygosity over three minisatellite loci	Clifford et al. 1998
	F had lower heterozygosity and fewer alleles	Cross & King 1983
	No difference in heterozygosity but F had lower gene diversity	Danielsdottir et al. 1997
	F had lower genetic variability relative to W	Mjølnerød et al. 1997
	F had lower genetic variability relative to W	Wislon et al. 1995

	F had lower heterozygosity and fewer alleles	Verspoor 1988
Pacific salmon and trout	F had fewer polymorphic loci, fewer number of alleles per loci and lower heterozygosity	Allendorf & Phelps 1980
	F1 Hy (between genetically isolated strains) had increased genetic variability	Gharrett & Smoker 1991
	F2 Hy demonstrated increased bilateral asymmetry	Gharrett & Smoker 1991
	F maintained high heritability for weight, indicating no reduction in genetic variability relative to W	Hershberger et al. 1990b

F = farmed, D = domestic, Hy = hybrid, W = wild

Pacific salmon

Loss of genetic variation was observed for isozyme loci in a cultured hatchery population of cutthroat trout revealing a 57% decrease in polymorphic loci, 29% reduction in average number of alleles per loci, 21% reduction in heterozygosity, and changes in allelic frequencies between age-class relative to the wild population from which they were derived 14 years earlier (Allendorf and Phelps 1980). Genetic differences between the reared and wild populations were as large as differences between natural populations.

Loss of genetic variability in domesticated fish has not been consistently observed. Coho salmon in a 10-year selection and breeding program demonstrated an increase of more than 60% increase in weight while maintaining high measures of heritability for weight (Hershberger et al. 1990). This study indicates that long-term selection programs can produce improvements in traits such as growth without dramatically reducing genetic variation. While direct molecular assessment of variation has not been reported for these populations, the retention of high heritability presumably arises from the overall breeding strategy undertaken in the domestication program for coho salmon in this case.

MECHANISMS OF GENETIC INTERACTION BETWEEN AQUACULTURED AND WILD FISH

Genetic effects of domestic fish may be direct or indirect. Direct genetic effects include the alteration of the wild genome (introgression) due to interbreeding between wild and domesticated fish or the production of sterile hybrids. Indirect effects include the effect of reduced effective population size or altered selection pressure arising from competition or the introduction of pathogens (Krueger and May 1991; Skaala et al. 1990; Waples 1991). Interbreeding between cultured and native populations has generally been found to be disadvantageous when the genetic effects alter fitness-related traits (Hindar et al. 1991). However, genetic effects of hybridization between farmed and wild salmon are somewhat unpredictable and may differ between populations. Most studies have focused on the fitness of the F_1 generation when exploring the effects of interbreeding between domestic and wild strains. Such hybrids may in fact have enhanced fitness due to hybrid vigor. A clearer picture would be provided by following the fitness of the F_2 and later

generations, as this in when outbreeding depression will begin to be expressed (see below). There is also limited information on the ability of introgressed genotypes to show an evolutionary response to environmental pressures. It is not known whether hybrid populations that phenotypically appear to be "wild" would evolve in a manner similar to true wild fish populations.

The genetic effect of escaped cultured fish on wild populations will depend on the demographics of the wild population, the magnitude and frequency of the escape, and the extent of introgression of aquacultured genotypes into the wild population (Hutchings 1991). The phenotype of wild and farmed hybrids may vary depending on the source of the wild population (for example see Einum and Fleming 1997).

ADDITIVE GENETIC EFFECTS

There is a growing body of literature indicating that phenotypic differences between domestic and wild fish are largely a result of additive genetic differences. Therefore, the phenotypic effects of domestication tend to be diluted with repeated backcrossing into wild populations. Interbreeding between farmed and native Atlantic salmon generally resulted in hybrids with intermediate expression of traits such as aggression, growth, and anti-predator behavior (Einum and Fleming 1997). McGinnity et al. (1997, 2003) found that first-generation and second-generation backcross hybrids were intermediate between wild and farmed Atlantic salmon in growth, survival, and parr maturity rates. For coho salmon, there is a strong correlation between the proportion of domestic genes within the genotype and measures of growth (McClelland et al. 2005; Tymchuk et al. 2006) and anti-predator behavior (Tymchuk et al. 2006). Introgression of domesticated and wild rainbow trout (Ayles and Baker 1983; Tymchuk and Devlin 2005) and chinook salmon (Bryden et al. 2004) show similar trends for growth and other measures of physiology such as disease resistance.

HETEROSIS

Crossing different strains with low genetic variability may re-establish lost alleles and allelic combinations, which could lead to hybrid vigor, or heterosis, wherein the F_1 generation would have increased fitness relative to the parental stocks. Heterosis is most likely to occur if the parental stocks are inbred and not highly genetically divergent. However, if the parent stocks came from different habitats, the resulting progeny may not be well adapted for either habitat. An allele that is advantageous in one genome or environment may be disadvantageous to overall fitness in another genome or environment. Cross-breeding experiments on five Norwegian strains of Atlantic salmon did not find significant heterosis for survival or body weight (Gjerde and Refstie 1984). Further experiments support a lack of heterosis for growth rate in Atlantic salmon fry (Friars et al. 1979). Heterosis for competitive ability may have been detected in hybrids of Atlantic and farm salmon in one instance, but the results are not clear (Einum and Fleming 1997). However, heterosis for growth and survival was detected when two different strains of brook trout were crossed (Webster and Flick 1981). Other studies on rainbow trout (including crosses among inbred lines) have detected evidence of heterosis for body weight (Ayles and Baker 1983; Gjerde 1988; Gjerde et al. 1983; Wangila and

Dick 1996). The introduction of low numbers of genetically novel fish into large populations may, in some cases, be beneficial by providing otherwise unavailable natural variation to the population which can be acted on by natural selection.

OUTBREEDING DEPRESSION

Outbreeding depression could cause a negative effect by disrupting co-adapted allele complexes, which would be indicated by the F_2 generation. The route of genetic introgression is likely to be through hybridization rather than by pure farm stock displacing pure wild populations, and thus outbreeding depression may not be apparent until recombination has separated co-adapted genotypes. Studies indicate that outbreeding depression can occur in fish populations. After following hybrids of genetically isolated pink salmon, the F_1 generation had increased genetic variability relative to the control fish, followed in the F_2 generation by very low survival and increased bilateral asymmetry indicating that outbreeding depression had occurred (Gharrett and Smoker 1994). Recent studies have confirmed the previous observation that outbreeding depression is possible in populations of pink salmon (Gharrett et al. 1999; Gilk et al. 2004). However, a study by McGinnity et al. (1997) undertaken to examine the survival and growth of farmed, wild, and hybrid Atlantic salmon in a natural environment, found no evidence for outbreeding depression as the fitness of the hybrid genotypes was intermediate between the farmed and wild genotypes. No evidence of outbreeding depression was found in crosses of wild coho salmon from different populations (Smoker et al. 2004) or during introgression of domestic and wild rainbow trout (Tymchuk and Devlin 2005) and coho salmon (Tymchuk et al. 2006). The difficulty in obtaining high statistical power in these experiments for estimates of outbreeding depression suggests that these negative results should be interpreted with caution until further data have been developed.

EFFECTS ON POPULATION SIZE AND INBREEDING DEPRESSION

Escaped cultured fish (possessing low genetic variability) may reduce the effective population size (Ne), leading to a population bottleneck and a concurrent founders effect. However, escapees could also increase effective population size if novel alleles are being added to a breeding group from distant populations. Analysis of microsatellite loci in wild and hatchery-reared brown trout used for enhancement purposes indicated reduced Ne and a loss of genetic variability (Hansen et al. 2000). A potential effect of reduced population size could be that native fish need to mate with genetically similar fish, leading to inbreeding depression. Inbreeding depression can occur in fish species as demonstrated in a study by (Gjerde et al. 1983) in which rainbow trout showed inbreeding depression for survival. Empirical studies have shown that inbreeding has a negative effect on fitness by causing a shift in fitness-related phenotypic traits. Another effect of increased difficulty in finding mates is the positive correlation between hybridization rates (for example between Atlantic salmon and brown trout) and the proportion of escaped farmed fish (Hindar and Balstad 1994).

EXAMPLES OF GENETIC INTROGRESSION OF CULTURED GENOTYPES INTO WILD POPULATIONS

Significant evidence now exists demonstrating the presence of aquacultured salmonids in nature. For example, initial rates of escaped farmed Atlantic salmon found in Norwegian rivers were as high as 70%, accounting for 1–15% of fish sampled in north and south Norway, respectively (Gausen and Moen 1991). Similarly, as salmon culture developed in SW Ireland, the number of escaped farmed fish entering salmon rivers was found to be substantial, making up to 70% of the catch in one river (Gudjonsson 1991), and in Northern Ireland, annual average proportions of farmed fish in the fishery ranged from 0.26–4.04% (mean 2.4%) in the marine environment and from 0.13– 2.62% (mean 0.89%) in freshwater (Crozier 1998). Since that time, continued evidence for the introgression of aquacultured salmonid genes into wild populations has been reported, including examples of native and non-native strains and species (Table 13).

Table 13. Examples of introgression of cultured genes into wild populations.

SPECIES	RESULT	SOURCE
Atlantic salmon	No genetic effect of F escape except in two small rivers near escape	Clifford et al. 1998
	Shift in allele frequencies of the W population towards that of the D; changes still present after two generations	Crozier 1993, 1998
	Introgression rates between 0.5% and 17.8%	Webb et al. 1993a
	Introgression rates between 1.9% and 12.3%	Webb et al. 1993b
Brown trout	W population genetically altered by interbreeding with D	Fritzner et al. 2001
	Evidence of genetic contribution from D in W population	Hansen et al. 2001

F = farmed, D = domestic, Hy = hybrid, W = wild

The effects of genetic introgression of farmed genotypes into wild populations will depend on how the natural genetic variation is distributed. Effects of introgression will be worse if much of the variation is distributed among populations and is associated with adaptive traits or reproductive barriers between stocks (Skaala et al. 1990). Anadromous populations of salmonids tend to be more resistant to introgression due to their more complex life histories (e.g. overlapping maturation age classes) as well as the sharing of genetic information that occurs through straying (Utter and Epifanio 2002). In addition, genetic distance between the two populations does not seem to be a reliable indicator of the potential effects of introgression (Utter and Epifanio 2002).

ATLANTIC SALMON

Following extensive escapes of farmed salmon in Scotland, a study was done to examine the extent to which these fish entered rivers and successfully spawned (Webb et

al. 1993b). Fry were sampled from 16 rivers near known escapes (River Polla in the previous year) to over 200 km away (throughout which range many other farms are also found). Using the presence of canthaxanthin (a pigment added to salmon feed, which is deposited in eggs) in the fry as an indicator of being derived from farmed mothers, 14 of 16 rivers showed evidence of farmed parentage. The average frequency of farmed progeny was 5.1%, ranging from 0.5–17.8% of the progeny sampled in different rivers. The values obtained in this study may underestimate the true introgression of farmed genotypes into populations, since contributions from paternal sources (which do not provide canthaxanthin to the embryo) would not be detected (Webb et al. 1993b).

A follow-up study was undertaken to determine the extent of introgression in the second year after an escape of farmed Atlantic salmon in Scotland (Webb et al. 1993a). Less than 0.5% of the escaped fish returned to the river to spawn, but the data indicated that fish may return for multiple years following an escape. Of 54 redds examined, five were found to contain progeny with canthaxanthin indicating farmed origin. An examination of rivers adjacent to the river Polla revealed the presence of canthaxanthin-bearing fry at frequencies of 1.9–12.3 % in the year of the escape as well as the year after. The authors feel that these levels of farmed progeny may be the background level of farmed spawning that is occurring in the rivers due to escapes other than the documented escape under study.

Farmed salmon escaped in the Glenarm River in Northern Ireland in 1990. An allozyme study indicated a shift in allele frequencies towards those in the farmed salmon, indicating that interbreeding had occurred (Crozier 1993). A follow-up study in 1997 indicated that even after two generations, the wild population was still significantly different from the pre-escape population. In addition, new alleles not previously detected were found, leading to the conclusion that further influxes of farmed salmon had occurred. Alternately, another study (Clifford et al. 1998) found little long-term (three years) genetic effect of a large-scale escape other than in two small rivers near the escape.

BROWN TROUT

Brown trout populations in Denmark have been found to be altered genetically by breeding with domesticated trout, as indicated by genetic differentiation analysis using microsatellite markers (Fritzner et al. 2001). In a similar study of brown trout, results indicated that while there was an absence of domesticated trout in the river, there was evidence of genetic contribution by the domesticated fish in the wild individuals (Hansen et al. 2001). In Spain, threatened populations of native brown trout are stocked with hatchery-reared fish and it has been found that the hatchery and wild fish do interbreed. Consequently, the genetic distance between the two strains (domestic and wild) has been seen to be decreasing at a rate of approximately 5% each year (Garcia-Marin et al. 1999). Similar effects have been noted in Norway, where the release of hatchery fish altered the genetic make-up of wild brown trout populations (Skaala 1992). Brown trout populations in the Mediterranean were examined for evidence of introgression from stocked domestic brown trout. Introgression rates varied from 0% –77% among test sites. Little natural variability was found to exist between native populations from the different sites, although introgression is increasing genetic variability and thereby increasing the

variability between populations. The concern is that native populations will eventually be replaced by uniform domestic stocks (Berrebi et al. 2000).

No reproductive barriers to genetic exchange were indicated after electrophoretic analysis of hybridization between introduced domestic and native populations of brown trout in the Mediterranean (Barbat-Leterrier et al. 1989). Rates of introgression ranged from 0–40%. Other studies support the observance of introgression between hatchery and wild populations of brown trout in the Mediterranean (Poteaux et al. 1999) although they argue that natural selection limits introgression by acting against hatchery and/or hybrid genes. However, several years post-stocking have still not eliminated the genetic differences due to introgression during stocking. Introgression between domestic and wild fish did occur in a stocked population of brown trout, and when compared with a population that had been previously stocked, there was a decrease in the presence of domestic alleles in the non-stocked population (Poteaux et al. 1998a). Allozyme analysis of four stocked and four unstocked populations of brown trout indicated varying levels of hybridization and introgression in both the stocked and protected areas, with evidence that hybrids can successfully reproduce past the first generation (Cagigas et al. 1999).

ATLANTIC SALMON X BROWN TROUT HYBRIDS

In the 16 rivers examined for presence of farmed salmon described in Webb et al. 1993a, evidence of brown trout x Atlantic salmon hybridization was also observed. All hybrids were the progeny of Atlantic salmon females by brown trout males based on analysis of mtDNA, and the incidence of hybrid vs. pure progeny from Atlantic salmon mothers was 4.3% hybrids for wild Atlantic mothers and 35% for farmed mothers (based on presence of canthaxanthin in progeny). This higher incidence of hybrid progeny from farmed mothers suggests a lower fidelity of spawning than for wild mothers (Youngson et al. 1993). Another study also found that hybridization between Atlantic salmon and brown trout varied with the status of the salmon population (Hindar and Balstad 1994).

PACIFIC SALMON

Over 70% of the fish farmed on the west coast are Atlantic salmon. There is little evidence that escaped Atlantic fish are capable of establishing naturally spawning populations, although there is some evidence of escaped farmed Atlantic salmon occasionally breeding in nature (Volpe et al. 2000). Laboratory-based studies indicate that the Atlantic escapees have such limited ability to interbreed with wild Pacific salmon that this is not considered a risk (Devlin unpublished, cited in Noakes et al. 2000). Interbreeding between cultured and wild Pacific salmon could potentially be a concern, but currently there is a lack of knowledge on the extent of introgression of farmed Pacific salmon into wild populations due to the difficulties of identifying cultured, wild and hybrid individuals. An examination of allele frequencies of rainbow trout in the Yakima River provided evidence of introgression from nonanadromous domesticated hatchery strains of rainbow trout (Campton and Johnston 1985). Similarly, evidence for introgression between native and hatchery rainbow trout was found in Metolius River, a tributary of the Deschutes River, Oregon (Currens et al. 1997). Introgression may not always occur, as one study found no evidence of introgression between hatchery and wild

chum salmon populations (LeClair et al. 1999). For coho salmon, wild spawners in the Samish and lower Nooksack rivers have been introgressed or replaced by hatchery-produced fish, whereas wild spawners in the upper Nooksack River show little influenced by gene flow from the hatchery strains (Small et al. 2004). Recent laboratory studies on introgression between cultured and wild Pacific salmonids have revealed that a large proportion of phenotypic divergence between the strains arises from additive genetic differences (Tymchuk *et al.* 2005, 2006; McClelland et al. 2005).

THE IMPORTANCE OF GENETICS TO CONSERVATION OF SALMONIDS

Genotype, in addition to environment, determines the adaptive phenotypic characteristics of salmonids, and as such it is likely that disruption of this genetic structure may have both short-term and long-term effects on individual fitness as well as the future resilience of populations to natural and anthropogenic pressures.

THE GENETIC CHARACTER OF WILD SALMONID POPULATIONS DEFINES THEIR CURRENT AND FUTURE ADAPTIVE PHENOTYPES

Significant evidence now exists demonstrating the unique genetic character of populations of several salmonid species. Native salmonid populations can be considered as genetically distinct stocks that have evolved adaptations to maximize fitness under selection regime of their local environments. Genetic differentiation among salmonid populations is well documented (King et al. 2001; Ståhl 1987) and in some cases can be correlated with adaptive phenotypes (Beacham and Murray 1987; Beacham et al. 1988; Clarke et al. 1995; Groot and Margolis 1991; Quinn 2005; Taylor 1991). Some genetically determined life-history traits of adaptive significance are known. For example, the age of smoltification in stream-type chinook salmon (Clarke et al. 1994), the populations of which tend to migrate to sea after spending at least one year in streams inland compared with coastal populations of ocean-type salmon, which migrate to the ocean in their first year. Another good example of a life-history adaptation is the nonanadromous form of sockeye salmon, kokanee. The two forms of sockeye can be found together in the same population, but seem to maintain their genetic identity through assortative mating (Foote et al. 1989) and reduced fitness of hybrids (Wood and Foote 1996)

Genetic differentiation of populations at the molecular level has been detected using allozymes and DNA markers in the mitochondrial and nuclear genomes (e.g. Billington and Hebert 1991; Krieg and Guyomard 1985, Ferguson 1989), and although such genetic differentiation among populations does not necessarily arise from selection, in many cases it does. For Atlantic salmon in Europe, genetic diversity both within and among populations has been correlated with performance characteristics relevant to survival and recruitment (Bourke et al. 1997; Verspoor 1997). Similarly, an examination of the genetic structure of wild and hatchery brown trout indicated that more than 60% of the genetic variability in the wild populations was due to differences between the populations (Garcia-Marin et al. 1991). In contrast, only 3% of the genetic variability for the hatchery fish was explained by differences between populations, demonstrating that

the hatchery fish represent a much more homogenous population with a narrower genetic base. Several species of Pacific salmon in British Columbia show clear evidence of genetic differentiation down to the subpopulation level (Beacham and Murray 1987; Beacham et al. 2002; Beacham and Withler 1985) and in some cases this differentiation is correlated with evolutionary significant units (ESUs) for the species (Wood and Foote 1996).

The homing behavior of salmon may facilitate genetic differentiation (which may occur by genetic forces in addition to selection), and indeed populations forced into genetic isolation (e.g. chinook salmon introduced into New Zealand from California approximately 90 years ago) already display evidence of phenotypic divergence between populations (Kinnison et al. 1998). Thus, natural populations carry unique reservoirs of genes and gene combinations, which are specially suited for providing adaptive phenotypes in the environment in which they evolved. Consequently, interactions between strains of fish with different genetic backgrounds are anticipated in some cases to genetically alter local native populations and reduce their viability by altering local phenotypic adaptations (Bams 1976; Verspoor 1998) and threatening intraspecific genetic diversity (Ryman 1997).

GENETIC VARIATION CUSHIONS EFFECT OF DELETERIOUS GENES

In addition to providing a cushion against extinction from environmental change, genetic variability in fish populations can hide deleterious recessive genes. Under non-equilibrium conditions, as the frequency of heterozygotes in the population decreases there is a loss of alleles and an increase in the expression of recessive alleles that may reduce survival when expressed. Indeed, heterozygosity, a measure of genetic variability, has been observed to be positively correlated with measures of fitness in several instances (Wang et al. 2002). For example, a study on six strains of hatchery-reared rainbow trout showed that higher heterozygosity related to faster development rate (as measured by hatching time) and egg size (Danzmann et al. 1985; Danzmann et al. 1986; Ferguson et al. 1985). In chinook salmon (Arkush et al. 2002) and rainbow trout (Ferguson and Drahushchak 1990) higher heterozygosity was associated with greater disease resistance. However, heterozygosity is not always correlated with fitness (Hutchings and Ferguson 1992).

GENERAL CONCLUSION

Escaped farmed salmon have made their presence known in the wild, and although their numbers may have a large variation, in general there is a positive correlation between the number of escaped farmed fish in the population and the size of the local aquaculture industry. Farmed fish demonstrate fitness-related differences relative to wild fish including less responsiveness to risk of predation and altered foraging strategies that tend to incur higher metabolic costs. For these reasons, and other considerations as discussed above, farmed salmon tend to have lower survival than wild fish. However, some farmed fish do survive and evidence indicates that these fish may be capable of successfully reproducing in the wild. As a consequence, the farmed fish may

successfully pass along their genetic material with a general trend of lower genetic variability in addition to altered fitness-related traits.

The genetic effects on interaction between cultured and wild fish populations will depend on the frequency and magnitude of escapes, their ability to interbreed with conspecifics, the size of the receiving population, and, most critically, the fitness of the domesticated genotypes in nature. Based on the present studies, the effect of a small introgression of farm alleles into a wild population would be anticipated to be diluted with repeated backcrosses in the absence of selection, and little phenotypic effect would be detectable after just two or more generations. In contrast, escapes of large numbers of farmed individuals into small populations, or repeated escapes of moderate numbers over several generations, would be anticipated to have an effect on the phenotype of the receiving population. The critical question – as yet unanswered – is whether natural selection can restore into such introgressed populations, genotypes yielding phenotypes and fitness well adapted for current and future environmental conditions.

GLOSSARY

Aquacultured – fish reared in culture throughout their entire life, usually for commercial purposes

Cultured – broad term referring to all fish not entirely reared in the wild; often applied to strains that have been reared throughout their entire life history in aquaria, such as in captive brood programs

Domestic – A formal definition of domestication was proposed by (Price 1984) as "that process by which a population of animals becomes adapted to man and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation"; domestication effects can be acquired very rapidly (within a single generation), and thus essentially all cultured fish may be at least partly domestic

Farmed – synonymous with aquacultured

Founder effect – chance change in the frequency of some genetic variants in populations as a result of a relatively small number of initial founders of the population

Genetic drift – random change in allelic frequencies that results from the sampling of gametes from generation to generation

Genotype x environment (G x E) interactions – Non-linear responses of phenotypes to environmental conditions observed among genotypes.

Hatchery – fish reared for part of their life history in hatchery facilities; usually produced from artificially spawned adult fish captured after returning from the wild, and are released back into the wild at various life history stages (depending on the species)

Heterosis – fitness of hybrids that exceeds the mean performance of the parental lines

Hybrid vigor – synonymous with heterosis

Inbreeding – non-random mating (with respect to genotype) where the mating individuals are more closely related than those drawn from the population by chance

Inbreeding depression – decline in mean fitness with increasing homozygosity within populations

Ne – effective population size; effective number of breeding individuals; number of individuals that would give rise to the calculated sampling variance if they bred as an idealized population

Norm of reaction – the phenotypic expression of a genotype under different environmental conditions

Outbreeding – non-random mating (with respect to genotype) where the mating individuals are less closely related than those drawn from the population by chance

Outbreeding depression – fitness of hybrids is below that of the parental lines

Plasticity – the environmentally sensitive production of alternative phenotypes by given genotypes.

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CULTURED AND WILD FISH DISEASE INTERACTIONS IN THE CANADIAN MARINE ENVIRONMENT

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EXECUTIVE SUMMARY

Intensive mariculture of fish is a recent industry in Canada relative to farming of land animals. This newness alone raises a unique set of questions and potential problems. Whenever there is a new use of the natural resources of an area, there is an inevitable alteration to that part of the environment being used. In the case of marine cage culture of fish, this is most obvious in the scenic sense and in the reduction of previously held rights to access by other users. However, other less apparent changes such as disease can also occur. In this context, the question frequently and justifiably asked is whether the changes due to the occurrence of infectious diseases in aquaculture introduce a significant or acceptable risk of detrimental effects to the environment and, in particular, to wild fish populations.

Over the last 20 years, several reviews have already comprehensively assessed the available scientific literature on the potential for disease interchange between wild and farmed fish (Hastein and Lindstad 1991; Brackett 1991; McVicar et al. 1993; McVicar 1997a, b; Hedrick 1998; Reno 1998; Amos et al. 2000; Amos and Thomas 2002; Olivier 2002). Notably, none of these reviews has found irrevocable evidence that fish farming has contributed to detectable adverse changes in wild fish populations, yet the topic remains one of the most controversial in the media and scientific community. The objective of this review is to focus on the main areas of potential risk using both the conclusions of individual authors who have reviewed the relevant literature and the outcomes of the different special workshops and conferences on the topic.

Disease in wild populations is rarely documented and therefore demonstrating changes in the patterns of disease in wild populations is challenging. As in any wild animal population, large numbers of different potential disease-causing agents can occur in any one species of fish. When epizootics do occur, clinically diseased specimens with high levels of infectious agents are usually easy to find, as was the case with the pilchard die-off in BC (Traxler et al. 1999). However, in comparison with farmed fish stocks, there are relatively few records of epizootics in wild fish. This cannot be interpreted as evidence of their absence or of a low level of risk of their occurrence. Highly pathogenic infectious agents that rapidly kill fish typically occur at low levels in non-epizootic situations.

Furthermore, carriers of infection without evidence of clinical disease are difficult to detect due to the size and inaccessibility of the environment. Finally, sick animals are rapidly removed by selectively high predation (McVicar 1997b).

Much more is known regarding disease interactions among the host, pathogen and the environment of cultured fish than wild fish populations because cultured fish are more easily observed. A dependence on unreliable data on the relationship between diseases in farmed and wild fish populations has often led to widely different interpretations of the same information, which in turn has further fueled the considerable controversy in this area. It is well established in Canada and elsewhere that there is not a unidirectional transfer of infection from either farmed fish to wild or vice versa, but that interchange of infection between the different environments is normal. There is a tendency for those with interests in aquaculture and with wild fish to focus on the route of transmission from one direction only. A major constraint to reaching robust conclusions on possible changes and effects of disease is a widespread lack of adequate information on the disease status of wild stocks prior to the establishment of aquaculture. The inability to compare fish disease patterns before and after the establishment of fish farming is a problem not only within Canada, but also internationally. Information on the extent of variation in naturally occurring disease is required before an assessment can be made on any effects that may be superimposed by infections in aquaculture. It is also difficult to prove a negative effect on wild fish populations since fluctuations in fish populations are normal, but the causes are multifactorial and complex. Unfortunately, the background information on natural variations is usually sparse from areas where fish farming is now being conducted. Information from areas with no fish farms can provide a general perspective of the natural levels of infection that can occur but should be treated with caution in the absence of sequential information on temporal and spatial variations.

Reports have indicated that a variety of pathogens are present in numerous marine fish species, which may then act as reservoirs for pathogens of farmed fish (Kent et al. 1998). The finding of infectious hematopoietic necrosis (IHN) virus in migrating sockeye salmon in seawater raises the possibility of a marine source or reservoir of the virus (Traxler et al. 1997), although there have been no reports of losses in wild salmonids in the marine environment due to viruses (Bakke and Harris 1998). The low density of salmonids in the marine environment reduces the potential for disease to affect populations. An understanding of the dynamics of infection and of the persistence of disease is necessary before conclusions can be drawn on the extent of any new risk being posed by the occurrence of disease in farms to local wild fish populations. Different host species that are capable of becoming infected may show a natural range of susceptibility to the same infection. Under high stress conditions (e.g., elevated temperatures, spawning), even the same host may show higher susceptibility to infection (Bernoth et al. 1997). These complexities in the interaction between the occurrence of infection in fish and the development of disease and the insufficiency of basic research have contributed in a major way to the uncertainties in the evaluation of the level of impact of diseases in fish farms on wild fish populations. In this context, the role of sea lice on farms has been extensively debated internationally, but a conclusion has not been reached in any country (McVicar 2004). Similarly, the impact of IHN virus on wild stocks of fish is an area that

is poorly understood and requires more research. As new aquaculture species are developed for culture in Canada, there will be a new opportunity to study disease interactions between wild and cultured species.

The introduction of new infectious agents into an area previously free of that infection could lead to serious outbreaks of disease (Olivier 2002; Kent 1994; Noakes et al. 2000). This can be due to the lack of an evolved resistance in the indigenous populations that may act as susceptible hosts. However, little can be done to prevent or restrict the natural spread of diseases associated with the normal movements of fish populations between areas or natural changes in distribution associated for example with climatic change. The focus must therefore be on human activities such as the transfer of live fish and eggs between aquaculture sites or where trade activities increase the risk of transferring infection significant to fish.

When wild fish are exposed to pathogens shed from farmed fish, neither infection nor disease is inevitable in the wild fish population. The following factors are critical: the occurrence and persistence of the infection in the source population; the availability of susceptible potential new hosts; the viability and concentration of the infectious organism in the environment; and the ability of the infection to affect the recipient population from individual fish infections (Olivier 2002). These complexities in the interaction between the occurrence of infection in fish and the development of disease and the insufficiency of basic research have contributed in a major way to the uncertainties in the evaluation of the level of impact of diseases in fish farms on wild fish populations.

The initial risk level of infection in wild fish associated with escaped farmed fish depends on the length of survival, behavior of the escaped fish after leaving the farm, and the reduced disease transmission opportunity in the lower fish densities outside the farm. Farmed fish in general are recognized to be maladapted to survival in the wild (Fleming et al. 2000) and the additional liability of fish carrying disease when they escape is likely to result in the early disappearance of the most seriously affected fish. The significance of the risk associated with diseased fish escaping from farms is therefore likely to be rapidly reduced towards levels equivalent to those for wild fish.

The introduction of new infectious agents into an area previously free of that infection can lead to serious outbreaks of disease (Kent 1994; Noakes et al. 2000; Olivier, 2002). Trade of live fish or eggs between areas carries risk of disease transfer as do other human activities such as processing where substantial concentrations of viable pathogens may be present. However, regulatory management steps taken by Canada has controlled this risk and the effectiveness of these actions is reflected in the fact that there are no recorded examples in Canada of any non-native fish diseases of concern being introduced either into farms or the natural environment.

Locally occurring diseases could get into farms principally through water, food or equipment. With the exception of treated or ground sources of seawater, fish farms are vulnerable to naturally occurring infections that are transmitted through water. It is more probable that the initiation of infections in marine fish farm is related to the level of

infection in the surrounding environment, such as that in wild fish, and the proximity of wild fish to fish farms. Diseases may be transmitted in water typically for short distances or through the escape of infected animals or through direct contact with infection sources (infected animal or other contaminated material). However, as the level of risk will vary considerably with different infectious agents and because of the complexity of factors influencing the initiation of infection and thereafter the development of disease, the simplistic view of risk being directly related to the level of exposure is not tenable.

During the early stages of marine salmonid farming in Europe, disease outbreaks due to bacterial infections (e.g., Vibrio *species) and parasites (e.g.,* Ichthyophonus*) were directly attributed to the use of fresh fish as a main source of food. The processing of manufactured feeds, which is used exclusively in current Canadian mariculture, destroys known infections of concern and is no longer as a source of disease.*

Although farm gear, including nets, graders, harvesting equipment, and even staff boots and clothing, can potentially transfer bacterial and viral infection between farms, the level of infection present on farms is usually sufficiently low that this is considered a relatively low-risk area compared with that associated with the transfer of live stocks. In epizootic disease situations particular caution has to be taken. Even in such circumstances, good farm management practices in relation to biosecurity measures can be effective in further reducing the level of risk and in helping to mitigate the possibility of future disease incidents.

The conditions such as crowding, which are typically found within a fish farm, are such that once infection is present there is risk of it spreading and causing a disease outbreak within the farm stocks. In this respect, fish farming is no different from intensive or semi-intensive farming on land. The development of effective vaccines in the fish farming industry has significantly reduced the problems associated with some of the serious diseases (Youngson et al. 1998). Where vaccines are not available, alternative disease management approaches have proved to be successful in reducing disease incidents on farms (McVicar 2004). Such approaches include, removing all fish from a farm facility to break disease cycles, area or bay management, and use of single generations and targeted administration of chemotherapeutants at critical times in the disease development cycle (e.g., of lice).

RECOMMENDED RESEARCH

- *Gaps in knowledge on potential disease hazards should be identified early and addressed through directed research based on the principles of risk assessment to provide options for their management in a structured manner.*
- *Baseline information on the disease status of wild stocks or a newly cultured species <u>prior</u> to the development of aquaculture in an area with emphasis on temporal and spatial variation would facilitate understanding of any effects that may be attributed to aquaculture.*

- *When a new species susceptible to a disease enzootic in native stocks is cultured, baseline information on pathogenicity and on wild-farmed fish disease interactions is desirable. An example would be nodaviruses in the family* Betanoviridae.
- *More information is needed on the cause–effect relationship in the transmission of disease between wild and cultured fish.*
- *Further studies are needed to objectively evaluate whether sea lice transfer between wild and cultured fish has any direct negative effect on the overall health of wild populations, particularly on the epizootiology of sea lice among Pacific salmon and its transmission to juveniles in inshore waters.*
- *Rapid diagnostic tests for IHN are needed. Studies on the factors involved in virus transmission and the susceptibility of other fish species should be conducted.*
- *Studies on waterborne disease agents or infective stages are needed to determine pathogen dispersion rates, since pathogens are frequently shed with feces.*

INTERACTIONS PATHOLOGIQUES ENTRE LES POISSONS SAUVAGES ET D'ÉLEVAGE DANS LE MILIEU MARIN AU CANADA

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RÉSUMÉ

La pisciculture marine intensive est une industrie nouvelle au Canada en comparaison de l'élevage d'animaux terrestres. La jeunesse même de l'industrie soulève une gamme unique de questions et de problèmes potentiels. Chaque fois que les ressources naturelles d'une région sont utilisées à de nouvelles fins, il faut se résigner au fait que la partie du milieu naturel utilisée sera inévitablement modifiée. Dans le cas de l'élevage de poissons en cages mouillées en mer, cela est particulièrement évident au niveau du panorama et des droits d'accès des autres utilisateurs. Mais d'autres changements moins apparents peuvent également se produire, notamment la manifestation de maladies chez les animaux aquatiques sauvages. Dans ce contexte, une question se pose fréquemment, pour de justes raisons, à savoir si l'occurrence de maladies infectieuses dans les installations aquacoles posent un risque important ou acceptable d'effets adverses sur l'environnement et, en particulier, sur les populations de poissons sauvages.

Au cours des 20 dernières années, de nombreux chercheurs ont effectué des études exhaustives de la documentation scientifique sur le potentiel de transmission de maladies entre les poissons d'élevage et les poissons sauvages (Hastein et Lindstad, 1991; Brackett, 1991; McVicar et al., 1993; McVicar, 1997a, b; Hedrick, 1998; Reno, 1998; Amos et al., 2000; Amos et Thomas, 2002; Olivier, 2002). Il est remarquable qu'aucun de ces chercheurs n'ait trouvé de preuves irréfutables que la pisciculture a contribué à des effets adverses décelables chez des populations de poissons sauvages. Malgré cela, ce point demeure l'un des aspects de l'aquaculture les plus controversés dans les médias et le monde scientifique. La présente étude documentaire porte sur les principales sources de risque potentielles. Elle est axée sur les conclusions de chercheurs qui ont passé en revue la documentation pertinente et les résultats de conférences et d'ateliers de travail sur le sujet.

Les maladies des poissons sauvages sont très peu documentées. Il est donc difficile de démontrer si des changements se sont produits dans la structure de la morbidité chez ces populations. Comme chez n'importe quel animal sauvage, un grand nombre d'agents pathogènes potentiels peuvent se manifester chez les poissons. Lorsqu'une épizootie se produit, des spécimens malades porteurs de niveaux élevés d'agents pathogènes sont

habituellement faciles à trouver, comme dans le cas de la mortalité massive de sardine du Pacifique en Colombie-Britannique (Traxler et al., 1999). Cependant, en comparaison des stocks de poissons d'élevage, relativement peu d'épizooties ont été documentées chez des poissons sauvages. Mais il ne faut pas interpréter cela comme une preuve de leur absence ou d'un faible risque d'occurrence. En premier lieu, les agents pathogènes hautement contagieux qui tuent rapidement les poissons sauvages sont typiquement présents à des niveaux faibles lorsque se produit une flambée de cas; en deuxième lieu, les poissons sauvages infectés qui ne montrent aucun signe clinique de maladie sont difficiles à déceler à cause de l'étendue et de l'inaccessibilité du milieu sauvage; et en troisième lieu, les poissons sauvages malades sont rapidement victimes des prédateurs (McVicar, 1987b).

Les interactions entre l'hôte, l'agent pathogène et le milieu d'élevage de poissons sont mieux connues que dans le cas des populations de poissons sauvages parce qu'il est plus facile d'observer les poissons d'élevage. La dépendance sur des données peu fiables sur la relation entre les maladies chez les poissons sauvages et les poissons d'élevage a souvent mené à des interprétations contradictoires des mêmes données, ce qui a fortement alimenté la forte controverse que le sujet soulève. Il a clairement été établi au Canada et à l'étranger que la transmission d'une infection d'un poisson d'élevage à un poisson sauvage ou inversement n'est pas unidirectionnelle; la transmission d'une infection entre milieux de vie est chose normale. Les parties intéressées à l'aquaculture et les parties intéressées aux poissons sauvages ont tendance à mettre l'accent sur la transmission unidirectionnelle. L'absence générale de données adéquates sur l'état de santé des stocks de poissons sauvages avant l'établissement de l'aquaculture empêche de tirer des conclusions robustes au sujet des changements qu'ils ont subis à cause des maladies et leurs effets potentiels. L'incapacité de comparer les patrons de maladie chez les poissons avant et après l'établissement de la pisciculture est un problème non seulement au Canada, mais aussi à l'étranger. De l'information sur l'ampleur de la variation des maladies naturelles est requise pour évaluer leurs effets potentiels lorsqu'ils viennent s'ajouter aux infections chez des poissons d'élevage. Il est en outre difficile de prouver que les infections chez les poissons d'élevage ont un effet néfaste sur les populations de poissons sauvages car ces dernières connaissent des fluctuations naturelles, dont les causes sont multifactorielles et complexes. Malheureusement, les données de base sur les fluctuations naturelles des populations de poissons sauvages trouvées dans des eaux où l'aquaculture est pratiquée sont rares. Une vue générale des niveaux naturels d'infection qui se produisent dans les secteurs libres de fermes aquacoles peut être établie à partir des données qui y ont été recueillies, mais, en l'absence de données séquentielles sur les variations spatiales et temporelles, il faut faire preuve de prudence.

Une gamme d'agents pathogènes sont présents chez de nombreuses espèces de poissons marins, qui peuvent ensuite servir de réservoirs d'agents pathogènes pour les poissons d'élevage (Kent et al., 1998). La découverte du virus de la nécrose hématopoïétique infectieuse (NHI) chez des saumons rouges lors de leur migration en mer soulève la possibilité de l'existence d'une source ou d'un réservoir du virus en mer (Traxler et al., 1997), bien qu'une mortalité de salmonidés sauvages en mer imputable à des virus n'ait

jamais été signalée (Bakke et Harris, 1998). Il est peu probable que les maladies aient une incidence néfaste sur les populations de salmonidés sauvages en raison de leur faible densité dans le milieu marin. Avant de pouvoir tirer des conclusions sur l'ampleur du risque que pose l'occurrence d'une maladie dans une ferme aquacole pour les populations locales de poissons sauvages, il faut comprendre la dynamique de l'infection et la persistance de la maladie. Diverses espèces hôtes peuvent montrer une vulnérabilité naturelle à la même maladie. Même un hôte soumis à un stress élevé (p. ex. température de l'eau élevée, reproduction) peut être davantage vulnérable à l'infection (Bernoth et al., 1997). La complexité de l'interaction entre l'occurrence d'une infection chez un poisson et le développement d'une maladie, ainsi que l'insuffisance de recherches de base, ont contribué dans une grande mesure aux incertitudes qui entourent l'évaluation du niveau d'impact des maladies qui se manifestent dans les fermes piscicoles sur les populations de poissons sauvages. Dans ce contexte, le rôle que joue le pou du poisson dans les fermes piscicoles a été longtemps débattu dans tous les coins du monde, mais aucune conclusion n'a été tirée (McVicar, 2004). De même, l'impact du virus de la NHI sur les stocks de poissons sauvages est un problème mal compris. D'autres recherches sont requises. Le développement de nouvelles espèces aux fins d'élevage au Canada constituera une opportunité d'étudier les interactions des poissons sauvages avec les poissons d'élevage sur le plan des maladies.

L'introduction d'un nouvel agent pathogène dans une région auparavant exempte de la maladie en question pourrait mener à de graves flambées de cas (Olivier, 2002; Kent, 1994; Noakes et al., 2000). Cela peut être imputable à l'absence de résistance acquise chez les populations de poissons indigènes, qui peuvent agir comme hôtes vulnérables. Toutefois, étant donné qu'il y a très peu de mesures à prendre pour prévenir ou limiter la propagation naturelle de maladies résultant des déplacements normaux des populations de poissons entre régions ou de l'agrandissement de leur aire de répartition, par exemple, à cause du changement climatique. L'accent doit donc être mis sur nos activités, comme le transfert d'oeufs et de poissons vivants entre sites aquacoles et les activités présentant des risques de transfert d'une infection qui pourrait nuire aux poissons, comme le commerce.

Lorsque des poissons sauvages sont exposés à des agents pathogènes issus de poissons d'élevage, il est impossible d'éviter que les poissons sauvages ne soient pas victimes d'une infection ou d'une maladie. Les facteurs suivants sont critiques : l'occurrence et la persistance de l'infection dans la population source; la présence de nouveaux hôtes potentiels vulnérables; la viabilité et la concentration de l'organisme infectieux dans le milieu; et la capacité d'un poisson malade d'infecter une population sauvage (Olivier, 2002). La complexité de l'interaction entre l'occurrence de l'infection chez les poissons et le développement d'une maladie, ainsi que l'insuffisance de recherches de base, ont contribué dans une grande mesure aux incertitudes qui entourent l'évaluation du niveau d'impact des maladies qui se manifestent dans les fermes piscicoles sur les populations de poissons sauvages.

Le niveau de risque initial d'infection de poissons sauvages associé à l'évasion de poissons d'élevage infectés dépend du temps de survie des évadés, de leur comportement

après l'évasion et de l'opportunité moindre de transmission de la maladie aux poissons sauvages, plus éparpillés dans le milieu naturel que ne le sont les poissons d'élevage. Les poissons d'élevage sont généralement reconnus comme étant mal adaptés à la vie dans le milieu sauvage (Fleming et al., 2000). Un poisson d'élevage malade qui s'évade a encore moins de chance d'y survivre. Il est donc probable que le niveau de risque associé à l'évasion de poissons d'élevage malades diminue rapidement jusqu'à un niveau équivalent à celui des poissons sauvages.

L'introduction d'un nouvel agent infectieux dans une région auparavant exempte de cette maladie peut mener à de graves flambées de cas (Kent, 1994; Noakes et al., 2000; Olivier, 2002). Le transfert interrégional d'oeufs et de poissons vivants pose des risques de transfert de maladies, tout comme d'autres activités, comme la transformation du poisson, car des concentrations élevées d'agents pathogènes viables peuvent être présentes. Toutefois, les mesures réglementaires prises par le Canada permettent d'enrayer ce risque. L'efficacité de ces mesures se reflète dans le fait qu'aucun cas d'introduction de maladies exotiques préoccupantes du poisson n'a été signalé dans les fermes aquacoles et le milieu naturel du Canada.

L'eau, les aliments et le matériel sont les principales voies potentielles d'entrée dans une ferme piscicole de maladies présentes au niveau local. À l'exception des sources d'eau de mer souterraine ou traitée, les fermes piscicoles sont vulnérables aux maladies naturelles transmises par l'eau. Il est plus probable que le déclenchement d'une infection dans une ferme d'élevage de poissons en mer soit relié au niveau d'infection dans le milieu environnant, comme chez les poissons sauvages, et à la proximité de ceux-ci aux fermes. Les maladies peuvent être transmises par l'eau, en général sur de courtes distances, à la suite de l'évasion de poissons infectés ou du contact direct de l'eau avec des sources d'infection (animaux infectés ou matériel contaminé). Toutefois, comme le niveau de risque variera considérablement selon l'agent infectieux et en raison de la complexité des facteurs qui influent sur le déclenchement d'une infection et le développement subséquent de la maladie, cette vue simpliste à l'effet que le niveau de risque est directement lié au niveau d'exposition n'est tout simplement pas défendable.

Au début de l'élevage de salmonidés en mer en Europe, les flambées de cas de maladies dues à des bactéries (p. ex. Vibrio *sp.) et des parasites (p. ex.* Ichthyophonus*) étaient directement attribuées à l'utilisation de poisson frais comme source principale de nourriture. Le processus de fabrication d'aliments industriels pour poissons, que l'industrie canadienne de la mariculture utilise exclusivement, détruit les agents pathogènes préoccupants connus. Les aliments ne constituent donc plus une source de maladie.*

Bien que le matériel de ferme, comme les filets, les trieurs, l'équipement de récolte et même les bottes et les vêtements des employés, puisse être à l'origine du transfert d'infections bactériennes ou virales entre fermes, le niveau d'infection dans les fermes est généralement assez faible pour que le matériel de ferme soit considéré comme ne constituant qu'un risque relativement faible en comparaison du risque associé au transfert d'oeufs ou de poissons vivants. Il faut cependant faire preuve de grande

prudence en cas d'épizootie. Dans de telles circonstances, de bonnes pratiques de gestion aquacole et des mesures de biosécurité peuvent se révéler efficaces pour réduire davantage le niveau de risque et prévenir d'autres épisodes de maladie.

Les conditions qui prévalent dans les fermes piscicoles, comme la densité élevée des poissons, sont telles que lorsqu'une infection s'y manifeste, elle risque de se propager et de causer une flambée de cas chez le stock mis en élevage. Sous cet aspect, la pisciculture ne diffère pas de l'agriculture intensive ou semi-intensive. Le développement de vaccins efficaces contre les maladies du poisson d'élevage a permis de réduire considérablement le nombre de cas de maladies graves (Youngson et al., 1998). Lorsque des vaccins ne sont pas disponibles, d'autres méthodes de lutte contre les maladies, comme le retrait de tous les poissons d'une installation piscicole afin de briser le cycle de maladie, la gestion de la région ou de la baie touchée, la mise en élevage d'une seule génération de poissons et l'administration ciblée d'agents chimiothérapeutiques au moment critique dans le cycle de développement d'une maladie ou d'un parasite (p. ex. pou du poisson) se sont révélées hautement fructueuses pour ce qui est de réduire l'occurrence de maladie dans les fermes piscicoles (McVicar, 2004).

RECHERCHES RECOMMANDÉES

- *Il faut identifier rapidement les lacunes dans les connaissances sur les maladies du poisson qui posent un risque potentiel en menant des recherches ciblées reposant sur les principes de l'évaluation du risque afin de cerner des options pour le gérer d'une manière structurée.*

- *Il faut recueillir de l'information de base sur l'état de santé des stocks sauvages ou de l'espèce nouvellement élevée avant de pratiquer l'aquaculture dans une région donnée, en particulier sur les variations spatiales et temporelles de l'état de santé, ce qui permettrait de mieux comprendre les effets de l'aquaculture.*

- *Lorsqu'une nouvelle espèce vulnérable à une maladie enzootique présente chez des stocks indigènes est mise en élevage, il faut recueillir de l'information sur la pathogénicité de cette maladie et sur les interactions au niveau de la maladie entre les poissons d'élevage et les poissons sauvages, par exemple, les nodavirus de la famille* Betanoviridae.

- *Il faut obtenir d'autres données sur la relation de cause à effet dans la transmission de maladies entre les poissons sauvages et les poissons d'élevage.*

- *Il faut mener d'autres études afin de pouvoir évaluer objectivement si le transfert de poux du poisson de poissons d'élevage à des poissons sauvages a un impact néfaste direct sur l'état de santé général des populations sauvages, en particulier sur l'épizootiologie du pou du poisson chez les saumons du Pacifique et sa transmission aux juvéniles dans les eaux côtières.*

- *Il faut mettre au point des tests de diagnostic rapide de la NHI. Il faut également mener des études sur les facteurs impliqués dans la transmission du virus et la vulnérabilité d'autres espèces de poisson.*

- *Afin de mieux comprendre le cycle de vie des myxosporidies marines, telles* Kudoa thyrsites *et* P. minibicornis, *il faut mener d'autres recherches dans le but d'élaborer des stratégies de prévention et de lutte efficaces contre ces parasites.*

- *Il faut mener des études sur les agents pathogènes d'origine hydrique ou leurs stades infectieux afin de déterminer leurs taux de dispersion, étant donné qu'ils sont fréquemment passés dans les excréments.*

BACKGROUND

Intensive mariculture of fish is a recent industry in Canada relative to farming of land animals. This newness alone brings a unique set of questions and potential problems. Whenever there is a new use of the natural resources of an area, there is an inevitable alteration to that part of the environment being used. In the case of marine cage culture of fish, this is most obvious in the scenic sense and in the reduction of previously held rights to access by other users. However, other less apparent changes can also occur, such as with disease. In this context, the question frequently and justifiably asked is whether the changes due to the occurrence of infectious diseases in aquaculture introduces a significant or acceptable risk of detrimental effects to the environment, in particular to wild fish populations. In addition, the aquaculturalist is concerned that any disease does not endanger the long-term sustainability of the facility.

Several reviews on the potential for disease interchange between wild and farmed fish have been published during the last 20 years (Hastein and Lindstad 1991; Brackett 1991; McVicar et al. 1993; McVicar 1997a, b; Hedrick 1998; Reno 1998; Amos et al. 2000; Olivier 2002), thus the available scientific literature in the subject area has already been comprehensively assessed. It is notable that none of these reviews has found irrevocable evidence that fish farming has contributed to detectable adverse changes in wild fish populations. Despite this, the topic remains one of the most controversial in the media and even in the scientific community.

Disease in wild populations is rarely documented. Demonstrating changes in the patterns of disease in wild populations presents numerous challenges. To establish a causal relationship between aquaculture and changing disease patterns in wild fish it is necessary to document variation from the pattern that existed before the development of aquaculture to verify that the pattern now occurring is not due to natural variation, and that it can be attributable to some feature of aquaculture. These objectives are difficult to achieve as it is well known that the determinants of disease in aquatic animals are multifactorial, interactive, and highly complex and that variations in the levels of disease are seldom due to changes in a single factor (McVicar 1997a, b; Olivier 2002).

When changes are thought to be occurring, defining an acceptable level of change requires solid evidence based on scientific principles, otherwise the belief of what is tolerable is then based on variable individual perceptions and often the level of personal involvement. No infectious disease of fish that has been found in Canada is unique to aquaculture. As all have a natural occurrence in the environment, the questions to be answered are:

- is there a detectable change in the natural occurrence or levels of disease because of an aquaculture development?
- what is the extent and consequence of any detected change?
- are any consequences significantly damaging to the sustainability of the environment?

It has to be said at the outset that the major constraint to reaching robust conclusions on possible changes and effects of disease is a widespread lack of adequate information on the disease status of wild stocks prior to the establishment of aquaculture.

The inability to compare fish disease patterns before and after the establishment of fish farming is a problem both within Canada and internationally. In addition, a dependence on unreliable data on the relationship between diseases in farmed and wild fish populations has often led to widely different interpretations of the same information, which in turn has fueled the considerable controversy in this area. The widespread reference to non-peer reviewed grey literature and the use of statements from the popular press as scientific evidence has contributed much to the confusion in this topic. There has also been a tendency to equate the frequency of repetition of a statement with its validity, without reference to the scientific legitimacy of its origin.

Biological science is often unable to accurately quantify the probability of relationships that are extremely unlikely or rare, even in closely controlled experimental situations. This difficulty is compounded in studies in the natural environment where wide variations can occur normally as a result of a wide range of causes. Thus, the possibility of establishing the absence of a cause and effect relationship between farms and disease variations being observed in the surrounding environment will not be easily achieved. In addition, it is accepted in the discipline of risk assessment that zero risk is not a realistic or achievable option (McVicar 2001). It is recognized that risks should be identified and managed to an acceptable level (MacDiarmid 2001). The World Trade Organization (WTO) Sanitary and Phytosanitary Agreement (SPS) recognizes that scientific justification is needed for trade restrictions among member countries for disease management reasons. The concept of an "acceptable level of protection" (ALOP) based on a structured risk analysis as outlined by the World Organisation for Animal Health, Office International des Epizootics (OIE, 2004) is now internationally accepted. The adoption of an approach requiring absolute proof of no risk of adverse effects from diseases in aquaculture prior to any development is therefore unrealistic if aquaculture is to be accepted as a valid use of the aquatic resource. As indicated above, studies on diseases in salmonid aquaculture worldwide have so far not provided evidence for major hazards to the viability of wild fish populations or other parts of the environment. However, information is still incomplete in many areas and vigilance must be maintained to detect any emerging problems that have not been previously suspected (e.g., through a structured reporting and investigation of diseases incidents. If gaps in knowledge are addressed through directed research based on the principles of risk assessment, any such potential hazards should be identified early and options for their management provided in a structured manner.

The objective of this review is to focus on the main areas of potential risk using both the conclusions of individual authors who have reviewed the relevant literature and the outcomes of the different special workshops and conferences on the topic. Instead of repeating the cover of available data, readers are directed to the reference lists in these documents. Concerns about aquaculture-related disease generally center on three main possibilities that:

- new diseases will be introduced into an area,
- there will be an abnormal elevation of levels of existing diseases and
- there will be the creation of atypical foci of disease both seasonally and geographically.

FISH DISEASE DATA RELEVANT TO CANADA

There has been a considerable increase in recent research on fish diseases worldwide, which has focused largely on the interest in health management in the developing aquaculture industries. Consequently, there is an accompanying extensive body of published data in the form of original research papers and specialist textbooks on farmed fish diseases. However, there is relatively little comparable information on disease in wild fish populations, largely because of the difficulty in collecting samples and to the more limited scope for the practical application of data in terms of fish health management. This imbalance can lead to a disproportionate and misleading impression of the occurrence and level of disease in farmed fish stocks.

Comprehensive reviews of the different groups of infectious diseases of fish can be found in a wide range of textbooks, including those by Woo (1995) and Woo and Bruno (1999). For salmonids, Hastein and Lindstad (1991) listed the diseases that may interact between wild and farmed populations. Such lists must be treated with considerable caution, as they do not necessarily inform on the level of hazard an infection may present in general and, most importantly, in the particular locality of interest. Commonly, one species of fish can harbor large numbers of different infectious agents (the scientific literature on wild Atlantic salmon lists over 80 different infectious conditions, ICES 1992), while individual wild fish can naturally carry high burdens of an infection without obvious detriment (e.g., more than 13,000 adult tapeworms in one fish as cited in McVicar 1977). Without some initial evidence of pathogenicity and of possible effects on the fish population, it would be a speculative and resource-demanding exercise to "bug hunt" for all possible infections in a fish species of interest in an area. It is widely accepted in Canada and elsewhere that there is not a unidirectional transfer of infection from either farmed fish to wild or vice versa, but that interchange of infection between the different environments is normal. The diversity of infectious agents described from fish (and the probability of many others as yet undetected) indicates that care must be taken in selecting those agents for further study as possible hazards. This is particularly true when new species of fish are being investigated for use in aquaculture. An understanding of the biology of the organisms, or related organisms, involved may provide some guidance. The principles of transmission, pathogenicity, host defense, and control of *Aeromonas salmonicida*, the causative agent of furunculosis, is provided by Bernoth et al. (1997) and illustrates a model of the type of data that may be required to support decision making in disease management. However, as diseases of potential significance vary considerably between different, even closely adjacent, areas and with different species of fish under cultivation, attempting to provide a comprehensive list focused on aquaculture in Canada is inappropriate.

Ideally, information is required on the extent of variation in naturally occurring disease and their consequences before assessment is made of any effects that may be superimposed by infections in aquaculture. Unfortunately, the background information on natural variations is usually sparse from areas where fish farming is now being conducted. Historic information, or data from areas where there are no fish farms, can be useful to provide a general perspective of the natural levels of infection that can occur. However, such data need to be treated with caution in the absence of sequential

information on temporal and spatial variations. Similarly, without a comprehensive knowledge of such variations within an area and over a prolonged period, studies of the pattern of infection in an area, as for example a prerequisite to establishing farming, are unlikely to be scientifically beneficial. The oceanographic and biological characteristics of an area will determine the extent of background data required to establish "normal" spatial and temporal patterns of disease incidence. This is exemplified with salmon lice *Lepeophtheirus salmonis*, which has been singled out as an infection of relevance to Canada in terms of potential wild-farmed fish disease interaction. This parasite has been sporadically reported from European wild salmonids in the scientific literature over the last century, prior to the development of fish farming (e.g., by Calderwood 1907; Shulman and Shulman-Albova 1953; Pemberton 1976) and in non-fish farming areas (e.g., by Malakhova 1972; Schram et al. 1998). In waters frequented by Canadian salmonid stocks, Huntsman (1918) noted *L. salmonis* on a large percentage of Atlantic salmon in traps in the Miramichi River in Northern New Brunswick, while White (1940, 1942) described lesions and mortalities caused by *L. salmonis* on Atlantic salmon spawning in the Moser River in Nova Scotia. Templeman (1967, 1968) recorded average lice infections of 2.7–7.5 in Atlantic salmon in 1965 and 1966 in the Labrador Sea, West Greenland Banks, Newfoundland Shelf and Grand Bank, stressing that these were likely minimal numbers because of rough handling of the fish during capture. Similar sampling difficulties were noted in studies in oceanic Pacific waters where the recorded average prevalence was over 6 in pink salmon and over 2 in chum salmon (Nagasawa 1987; Nagasawa et al. 1993). The high infection levels (mean intensity of 300) found by Johnson et al. (1996) on sockeye salmon associated with a delayed freshwater migration in the Alberni Inlet, BC, in the early 1990s illustrates the difficulties in distinguishing a "natural" event from a possible aquaculture-associated variation. In an effort to resolve some of the considerable controversy that has been gathering around the topic of disease interactions between farmed and wild fish, several national and international scientific meetings have been convened within the last few. These have occurred, for example, the International Council for the Exploration of the Seas (ICES) in 1996; ICES and the North Atlantic Salmon Conservation Organisation (NASCO) in 1997; and a Canadian Regional Assessment Program (RAP) in a Workshop in 1998. These assemblies have focused mainly on salmonids, specific disease conditions, and on defined locations. Reports from these meetings (ICES 1997; Youngson et al. 1997; Ritter 1999; DFO 1999) and papers reviewing the literature (e.g., Hastein and Lindstad 1991; McVicar 1997a, 1997b, 2004; Olivier 2002) provide comprehensive coverage of the available scientific literature in the topic area, much of which is directly relevant to Canada. More recently, international information on sea lice in fish farms in relation to wild salmonid populations was considered in Canada at a Sea Lice and Open Science Forum held in Vancouver, British Columbia in February 2003 and at an International Conference on the Biology and Control of Sea Lice held in St Andrews, New Brunswick in July 2003. Despite the abundance of new information on sea lice, the controversy on the inter-relationships between infections in farmed and wild salmonid populations has yet to be resolved.

NATIONAL DATA

EAST COAST

Olivier and MacKinnon (1998) reviewed the relevant literature on potential impacts on wild salmon stocks from diseases attributed to farmed salmon operations in the Atlantic Provinces as part of the RAP Workshop covering all aspects of potential interaction between salmon farming and the surrounding environment. They concluded that serious disease incidents rarely occur in wild fish populations and are possibly cyclic in some non-salmonids. In a well-documented example, Sindermann (1958, 1966) noted that several epizootics of *Ichthyophonus* occurred in Atlantic herring *Clupea harengus* in the Gulf of St Lawrence and Gulf of Maine accompanied by severe mortalities in the late 1950s and early 1960s. For cases of disease impacts on wild salmonid stocks, Olivier and MacKinnon (1998) included ulcerative dermal necrosis (UDN), furunculosis, and *Gyrodactylus salaris* in Atlantic salmon in freshwater in Europe, whirling disease in juvenile rainbow trout in the US, and infectious hematopoietic necrosis (IHN) virus in western North America. Although disease interaction between wild and cultured fish was also noted, these authors concluded that there was no evidence that the decline in wild Atlantic salmon populations in the Maritimes region was the result of diseases from farmed fish. The report of the RAP Workshop (DFO 1999) noted that "The impact on wild fish populations of infectious diseases identified in the Maritimes is unknown," and recommended research initiatives into the upgrading of fish health information and procedures (particularly pertaining to wild fish health status, mechanisms of disease transfer and diagnosis).

Olivier (2002) later revisited this subject area, extending the consideration beyond salmonids to other species of farmed and wild fish, and came to the same conclusions. In particular, he noted that "... there is no documented evidence to substantiate the hypothesis that wild Atlantic salmon populations are declining in the Atlantic Provinces as the result of the spread of disease originating from farmed fish." Despite data existing for transfer in both directions between wild and farmed fish, there is a tendency for those with interests in aquaculture and with wild fish to focus on the route of transmission from one direction only. Olivier advocated further investigations using risk assessment methods to enable all concerned to make better-informed decisions.

The viral disease, infectious salmon anemia (ISA) was detected in the salmon farming industry in New Brunswick in 1997. Since then, there have been recurring outbreaks on an annual basis, although the effects on the industry have been reduced greatly by the management program introduced (Olivier and MacKinnon 1998). The finding of ISA in wild salmon caught in the same river trap as affected escaped salmon in the Magaguadavic River in New Brunswick illustrates the difficulties in determining the source and significance of infection. In the Maritime Provinces, wild Atlantic salmon have been tested for the presence of ISA since 1997. Starting in 1998, wild Atlantic salmon have, on occasions, tested positive for the ISA virus. However, these positive results were obtained using the very sensitive molecular method (RT-PCR), which detects genomic fragments of the virus. Clinical disease was never observed and the ISA virus has not been isolated from any wild salmonids with the exception of the Magaguadavic River wild salmon mentioned above (A-M MacKinnon, unpublished

results). To date, the significance of these positive RT-PCR results remains questionable. Olivier (2002) noted that the perception that ISA could have a potential significance on wild salmonids was not supported by evidence from the areas where outbreaks had by then occurred. As ISA is a disease listed as "significant" by the Office International des Epizooties (2004), the current international distribution of outbreaks are well detailed: the disease has now been reported from Norway, eastern Canada, Scotland, Chile, Faroes, eastern US, and Ireland (Miller and Cipriano 2003). Within a country, the spread of ISA between farms from an initial outbreak has been linked to aspects of the fish farming (Jarp and Karlsen 1997; Stagg et al. 2001; Murray 2003). No links have been established between these outbreaks in the different areas and epizootic studies have indicated the ISA virus might exist within a widely distributed wild host (Stagg 2003). The widespread distribution of ISA on both sides of the Atlantic and in the south Pacific suggests that there is a risk that this disease could be naturally present in other areas such as in BC and at some time could appear in currently unaffected salmon farming industries.

With specific reference to the New Brunswick salmon farming industry, Stewart (1998) reviewed the disease agents and diseases present, evaluated factors that cause infection of each agent to progress to overt disease and weighed the risk factors involved in disease transmission between farms. The general point made that is of direct relevance to the current paper was that when fish share water, there is a risk of shared disease. He noted that there are limited data available to flesh out this maxim in practical terms.

As new aquaculture species are being developed for Canada, there may be an opportunity to study disease interactions between wild and cultured species. Before a species susceptible to a disease enzootic in native stocks is cultured, baseline information could be obtained on pathogenicity, followed by studies on wild-farmed fish disease interactions. For instance, nodaviruses, in the family Betanoviridae, are becoming increasingly recognized as serious pathogens of finfish and crustaceans causing a variety of diseases. In finfish, viral encephalopathy and retinopathy (VER) or viral nervous necrosis (VNN) is found in many species, several of which are cultured. Also, as new aquaculture species are being developed, diseases caused by these viruses could be a major constraint (Munday and Nakai 1997) with the disease(s) linked to several viral groupings (such as striped jack nervous necrosis virus (SJNNV), tiger puffer nervous necrosis virus (TPNNV), barfin flounder nervous necrosis virus (BFNNV), and red-spotted grouper nervous necrosis virus (RGNNV)). There appears to be a strong correlation of genetic similarity of nodavirus isolates within a geographic location. A nodavirus isolate obtained from winter flounder in New Brunswick appears to be more genetically similar to those isolated from haddock and cod in Atlantic Canada than isolates obtained from other flatfish species in Europe and Asia (Gagne et al. 2004). The mortality rate for many of the host species is reported to be 80–100% depending on age of the fish with the highest rates observed for younger life stages. The viruses appear resistant to environmental conditions and without appropriate care, could readily be transported to new areas through commercial activities, especially since vertical transmission has been experimentally demonstrated in sea bass (*Dicentrachus labrax*) (Breuil et al. 2002) and is known to occur in other species such as jack (*Pseudocaranx dentex*) (OIE 2004).

Recent surveys in Atlantic Canada have shown a low prevalence of piscine nodavirus in wild winter flounder, *Pseudopleuronectes americanus*, in New Brunswick

(Barker et al. 2002). Two years following this finding, a genetically similar isolate caused an epizootic in cultured juvenile haddock in the same vicinity (Mackinnon unpubl.). The potential for wild fish to serve as a possible reservoir of infection cannot be eliminated in this case since the hatchery influent was untreated seawater and in some species asymptomatic carriers have been shown to shed the virus (Castric et al. 2001). In Norway, Bergh et al. (2001) speculated that VER is the reason halibut fry production has not increased since 1995. There are also reports (Grotmol 2000) that certain nodaviruses may be pathogens of salmonid species and have been associated with cardiac myopathy syndrome in Atlantic salmon.

While much remains to be learned about this grouping of viruses (e.g., route of transmission, temperature requirements, age and host susceptibility), there is an unknown risk that incursion of such a disease into aquaculture could affect individuals or populations of susceptible wild stocks in the area, especially if juvenile fish are present in areas with culture facilities. Conversely, the findings by Barker et al. (2002) indicate that the success of culturing susceptible species in Canada could be severely influenced by the presence of infected wild stocks.

WEST COAST

The salmon farming industry started in BC in the late 1970s initially farming local salmonid species (chinook and coho). By the mid-1980s, the industry switched to farming Atlantic salmon, and by 2002 approximately 80% of the product raised was Atlantic salmon with chinook making up most of the remaining 20% (www.salmonfarmers.org/ June 2005) (http://www.salmonfarmers.org/library/farm.html). In 1997, the Government of BC through its Environmental Assessment Office (EOA) completed a thorough review of the salmon farming industry in response to public concerns relating to escapes of farmed fish, fish health, waste discharge, interactions between salmon farms and coastal mammals, and farm siting (British Columbia, 1997). Comprehensive discussion papers were prepared by experts on a technical advisory team (TAT), who made recommendations on these key issues based on their review of the situation in BC and abroad. In general terms, and based on the BC farming practices of the time, the team concluded that salmon farming presented a low risk to the environment. In the area of fish diseases, the TAT identified significant gaps in the understanding of disease both in wild and cultured fish. They state that while "The susceptibility of farmed salmon to diseases may be increased by the stress of being raised in captivity," [it is unknown] "whether there is a greater incidence of disease in farmed fish than in wild fish." It was also stated that, "there is no evidence to prove or disprove whether transfer of pathogens and parasites from farmed to wild stock increases the rate of disease," however, "current evidence suggests [...] that diseases are not transferred from farmed to wild fish." They suggest that more precise information on causal relationships is required. To assist with the management of fish health and proactively address health problems in the BC aquaculture sector, the reviewers made nine recommendations:

- Establish a fish health working committee to promote, integrate and incorporate fish health policy development in BC;
- Strengthen disease surveillance and control programs;

- Develop standards for managing farmed salmon health as part of a salmon aquaculture code of practice, and enforce the standards as a condition of the salmon aquaculture licence;
- Improve the quality and accessibility of fish health information;
- Strengthen policies and programs respecting importation;
- Strengthen the requirements for sampling and reporting of diseases in fish being transferred within BC;
- Enhance fish health inspection practices at fish processing facilities;
- Strengthen control of drug use on salmon farms; and,
- Ministry of Health and Health Canada should undertake further review of issues related to antibiotic and other drug use at salmon farms.

While the review was targeted at salmon culture in BC, many of the recommendations would apply equally to other jurisdictions and to other species being cultured. Since the completion of the review, federal and provincial agencies have worked on putting the recommendations into place. For example, the aquaculture industry, with federal and provincial input, has developed a fish health database that collects data from individual farms as well as federal and provincial fish culture facilities. Amalgamated information is publicly available and reports from the information are planned. Standards for managing farmed salmon health are in place through site-specific fish health management plans.

More recently, the Pacific Fisheries Resource Conservation Council (PFRCC) also reviewed salmon farming in BC with special emphasis on sea lice and declines of pink salmon in the Broughton Archipelago in 2001/2002. In response to significant public concerns about the finding of high levels of sea lice on outmigrating pink salmon by local fishers in 2001, and as a result of substantial decreases in pink salmon escapements in 2002, the PFRCC issued two reports: 2002 Advisory: the Protection of Broughton Archipelago Pink Salmon Stocks, and the 2003 "Making sense of the Aquaculture debate: Analysis of issues related to netcage salmon farming and wild salmon in British Columbia" (both available at www.fish.bc.ca July 2005). On fish health, the key conclusions were:

- sea lice from fish farms constitute the most serious and immediate risk;
- bacteria pose the lowest risk to wild salmon of all fish health issues considered; and,
- viruses pose lower health risks than do sea lice, but higher risks than that of bacteria.

They reached a conclusion on sea lice despite the absence of "absolute proof directly linking the spread of sea lice from farmed to wild populations." Scientific conclusions are extremely diverse in the available literature, however while it is clear that lice will be transferred between wild and cultured stocks, any direct negative effect on the overall health of wild populations has yet to be demonstrated (ICES 1997; Heuch et al. 2005).

Prior to the PFRCC conclusions, Kent et al. (1998) compared the prevalence of *Renibacterium salmoninarum*, *Loma* spp, epitheliocystis, viral haemorrhagic septicaemia

(VHS) virus, IHN virus, and *Aeromonas salmonicida* in 81 fish species in the marine environment near farms and at a distance from farms. While they did not specifically study sea lice, almost all of the fish surveyed were clinically normal. While the authors comment that it is "well documented that wild fish may act as reservoirs for certain pathogens afflicting netpen farms," they state "the data does not indicate transfer of pathogens from netpens to wild fish populations (or vice versa)."

The two primary issues raised by the EAO and PFRCC are 1) the risk of introducing a pathogen into a new environment in which local stocks have not developed an immunity to the exotic disease agent, and 2) the introduction of an exotic host that is highly susceptible to an enzootic disease agent. The introduction of Atlantic salmon to the British Columbia coast is such an example. Atlantic salmon have no innate immunity to IHN virus and major epizootics have occurred in farmed fish since 1992 (Armstrong et al. 1993; Traxler et al. 1993; St-Hilaire et al. 2001). Although IHN virus is widely carried by sockeye salmon in British Columbia, epizootics in Pacific salmon are rare and tend to occur during the swim-up stage before fish develop naturally acquired immunity. Unlike Atlantic salmon, Pacific salmon have co-adapted with IHN virus and studies of susceptibility have shown that resistance to the virus increased with size and age (LaPatra 1998; LaPatra et al. 1990). This increased resistance to IHN virus in larger fish is not observed in farmed Atlantic salmon with cumulative losses exceeding 50% being observed in fish up to market size of over 5 kg (Saksida 2003).

Given the IHN outbreaks and ongoing disease on farms in 2001–02, the effect on surrounding wild stocks, both salmonid and non-salmonid, must be considered. As stated earlier, we tend to know much more regarding disease interactions among the host, pathogen, and the environment of cultured fish than we do regarding wild fish populations because cultured fish are more easily observed. The epizootiology of diseases in captive populations is more easily studied than in wild populations where diseased fish are removed from the population by predation and dead fish are usually not available for study. Despite these difficulties there have been numerous documented occurrences of diseases in wild fish populations on the Pacific coast of North America in both freshwater and seawater (Williams and Amend 1976; Traxler 1986; Traxler and Rankin 1989; Traxler et al. 1998; Meyers et al. 1994).

Little is known about the implications of disease on populations of wild salmon in the marine environment since the few studies conducted on the prevalence of disease agents have been surveys of apparently healthy fish. Reports of the presence of pathogens in marine fish have indicated that a variety of fish pathogens are present in numerous species of marine fish that may act as reservoirs for pathogens of farmed fish (Kent et al. 1998). The finding of IHN virus in migrating sockeye salmon in seawater raises the possibility of a marine source or reservoir of the virus (Traxler et al. 1997). In spite of this finding, there have been no reports of losses in wild salmonids in the marine environment due to viruses (Bakke and Harris 1998). It is difficult to prove a negative effect on fish populations in a natural environment where wide deviations in population numbers normally occur and causes are multifactorial and complex. These effects may be further confounded by the effects of human activities such as fishing pressures. The low density of salmonids in the marine environment makes the chances of disease having a negative effect on populations less likely. However, IHN virus has frequently caused high losses among juvenile sockeye salmon in freshwater (Williams and Amend 1976, Traxler

1986; Traxler and Rankin 1989; Follet and Burton 1995) where fish are more easily observed and are more susceptible than in the marine phase. There have also been mortalities associated with IHN in 2-year-old wild kokanee (landlocked *Oncorhynchus nerka*) populations (Traxler 1986, Traxler 1988). In the marine environment the North American strain of VHS virus, which is enzootic on the Pacific coast, has caused significant losses among Clupeidae species (Meyers and Winton 1995; Hershberger et al. 1999; Traxler et al. 1999; Hedrick et al. 2003). These losses have often been associated with temperature, nutritional, and/or maturation stresses in Pacific herring (*Clupea harengus pallasi*) and sardines (*Sardinops sagax*), which tend to school in high densities where pathogens are more readily transmitted.

IHN and its causative virus, IHNv, was the topic of an industry-government-academia international workshop in 2003 . The White Paper that came out of the meeting identified priority research needs such as better diagnostic tests, disease control strategies including effective vaccines, and determination of risk factors for transmission and disease outbreaks. Research done on many of the topics will also assist in answering questions on disease interactions between wild and cultured stocks. Work on disease prevention, for instance vaccination, will minimize the interactions. Members of the workshop also agreed that IHN can be used as a model system for the disease problems facing the West Coast industry. Hence, answers to IHN questions may apply to other disease outbreaks.

A Sea Lice and Open Science Forum were held in Vancouver in February 2003 to review the biology of salmon lice and related management strategies, identify knowledge gaps, and identify research required. Immediate actions noted as being essential included local consultations, lice-monitoring programs on wild and farmed fish, a review of treatments used internationally, identification keys for lice and communication. Several of these actions were already in place, and results are posted online as data from surveys undertaken by the DFO and BC Action Plans on Sea Lice are obtained (www-sci.pac.dfo-mpo.gc.ca/mehsd/sea%20lice/pink_salmon_e.htm and www.gov.bc.ca May 2005). Since 2003, considerable research activity has targeted knowledge gaps relating to sea lice in coastal British Columbia. While the extent and significance of sea lice interactions between cultured and wild salmon populations are not yet established, there is a growing awareness of the importance of salmonid and non-salmonid wild hosts and local oceanographic features in the epizootiology of *L. salmonis* in the region (Jones and Nemec 2004; Beamish et al. 2005; Brooks 2005; Jones et al. 2006).

The myxozoan parasite *Kudoa thyrsites* is enzootic in the muscle of several wild salmonid and non-salmonid species in coastal waters of British Columbia (Kabata and Whitaker 1989; Moran and Kent 1999a). The parasite occurs in the skeletal muscle of marine netpen-reared Atlantic salmon where it is associated with postmortem myoliquefactive autolysis that reduces the flesh quality (Whitaker and Kent 1991; St-Hilaire et al. 1997). Although the life cycle and route of transmission of *K. thyrsites* have not been established, farmed Atlantic salmon become infected by exposure to the same naturally occurring infectious stages that maintain infections in wild reservoir hosts (Moran and Kent 1999b). It is unlikely that infections in pen-reared Atlantic salmon contribute significantly to infections in wild species since dead fish are removed from netpens before spores are released through decomposition. The parasite is microscopically detected in fresh muscle or following histological preparation of fixed

tissue. Polymerase chain reaction is useful in detecting infections of low intensity and a recently developed digoxygenin-labelled oligonucleotide probe may be useful in identifying early developmental stages of the parasite in the salmon (Jones et al. 2003a).

Parvicapsula minibicornis (Myxozoa: Parvicapsulidae) is parasitic in the kidney of adult sockeye, pink, chinook and coho salmon migrating in the Fraser River (St-Hilaire et al. 2002; Jones et al. 2003b). Pathology associated with severe infection is associated with prespawning mortality among certain sockeye stocks (Raverty et al. 2000). Although the life cycle is not fully understood, epidemiological evidence strongly suggests that transmission occurs in the lower Fraser River or estuary (St-Hilaire et al. 2002). There is no evidence that this parasite occurs in netpen-reared Atlantic salmon in BC. An unrelated species, *Parvicapsula pseudobranchicola*, was associated with mortality in netpen-reared Atlantic salmon in Norway (Karlsbakk et al. 2002). An important knowledge gap that applies both to *K. thyrsites* and *P. minibicornis* is our poor understanding of the life cycles of marine myxozoa. This information is necessary to develop effective prevention and control strategies and assisting in the management of wild populations.

Declines in fish populations are observed worldwide. Reasons for the declines are generally speculative. Noakes et al. (2000) commented on a variety of potential causes for the decline of Pacific salmon abundance along the West Coast of Canada. The most likely reasons given were a combination of climate change, overfishing, and freshwater habitat destruction. They reviewed the disease aspects of farming and enhancement projects and concluded that while farmed salmon are a potential source for some pathogens, surveys of wild and hatchery fish show no pattern that could be attributed to salmon farming (www.gov.bc.ca September 2005).

INTERNATIONAL DATA

In 2001, the United States National fisheries agencies undertook a review of salmon farming in the Pacific Northwest, which detailed possible risk factors (Nash 2001). Fish health topics evaluated were the proliferation of fish and shellfish pathogens in the aquatic environment, and the increased incidences of disease among wild fish.

The author concluded that both of the topics presented a low risk to the environment and fish/shellfish stocks. The report stated that: "The specific diseases and their prevalence in Atlantic salmon stocks cultured in netpens in Puget Sound are not shown to be any different than those of the more numerous cultured stocks of Pacific salmon in hatcheries, which in turn are not known to have a high risk for infecting wild salmonids."

In 1997, ICES and NASCO convened a symposium on "Interactions between Salmon Culture and Wild Stocks of Atlantic Salmon: The Scientific and Management Issues." This was in recognition of the rapidly developing Atlantic salmon farming industries in several countries and the growing knowledge regarding interactions between farmed and wild stocks. Relevant scientists evaluated the state of current knowledge of these interactions and considered the implications for management and for future research. A series of scientific papers from the meeting was published in the ICES

Journal of Marine Science, 54 (1997). In the published report, Youngson et al. (1998) provided a summary of the session on disease and parasite interactions:

> Contagious diseases are one of the largest and most serious problems in the fish farming industry. Although diseases also occur in wild fish, they can usually be regarded as a phenomenon, rather than a problem, and they existed long before the commencement of fish farming. Releases of hatchery smolts or escapement of salmon from fish farms are potential ways of spreading infectious diseases and parasites that are harmful to wild stocks. Movement of fish between localities increases the risk, in particular when the movements are over long distances to river systems isolated from the area where the pathogens and fish evolved and became co-adapted. Examples of the spread of infectious diseases/parasites are the introduction of furunculosis from Scotland to Norway and the introduction of the parasitic fluke *Gyrodactylus salaris* from the Baltic Sea to several countries in the Scandinavia and Russia. Although there is no scientific evidence of adverse effects of salmon lice on wild Atlantic salmon, results from research with sea trout suggests they cannot be ruled out.

In their conclusions on the symposium, Youngson et al. (1998) noted that through the development of effective vaccines, the fish farming industry had significantly reduced the problems with some of the serious diseases. However, they believed there remain serious risks of transmission of fish parasites and that fish culture could still act as a vector for the spread of diseases. In the same report, Youngson et al. (1998) reported to NASCO that although current national and international legislation and codes of practice were established to protect zones free from listed diseases, this area remained a continuing priority area of concern. Similarly, although most enzootic diseases were noted as being under control in fish farms, the exception of sea lice caused concern and controversy regarding the possibility that this infection may be amplified within salmon farms, with subsequent detrimental effects to local populations of wild salmon. It was noted that foci of lice infection occurred in the immediate vicinity of infected farms, in river estuaries, and at a lower level in the open sea (on both trout and salmon). Youngson et al. (1998) identified a need for the application of proper experimental design to assess cause–effect relationships of lice/host interactions. They challenged scientists, farm managers, and governments to maintain scientific objectivity (i.e. use of the null hypothesis) and to use this knowledge to develop procedures to contain and control adverse effects for both salmon farmers and recreational fisheries interests. The review paper at the meeting on disease and parasite implications of the coexistence of wild and cultured Atlantic salmon (McVicar 1997b) concluded that there were no reports linking significant disease problems in wild stocks with environmental effects of fish farming, or with farmed fish escaping. However, the controversy surrounding salmon lice had not been resolved, largely because the leading scientists in the field were tending to select the opposite extremes of the options available for the interpretation of data.

As noted above, in 1996 ICES convened a special topic workshop on the "Interactions between Salmon Lice and Salmonids" to address the increasing interest in the topic of interactions between the developing mariculture industries and the surrounding environment in European and North American waters. In particular, this workshop addressed the need to deal with the considerable controversy surrounding the subject of salmon lice populations in salmon farms possibly adversely affecting the populations of wild salmonids in the fish farming areas. A total of 31 invited scientists,

all then currently active in research on sea lice and on wild salmonid populations, attended from Canada, Norway, Russia, UK, Ireland and the Faroes. All relevant scientific data were open for evaluation. Despite this focus of the world's expertise on the topic area, the report of the workshop (ICES 1997) contained only limited conclusions. The difficulty that participants found in establishing reasonably probabilities of cause–effect relationships from the information available prevented a consensus view on many of the questions raised. However, agreement was reached that the later developmental stages of salmon lice are significantly pathogenic, that the early return of sea trout post-smolts to freshwater can be associated with sea lice infestation and that lice emanating from fish farms may transfer to wild trout populations. Data on the extent that transfer from farm to wild populations occurs could not be quantified.

The salmon farming industries in Europe and North America have been put under considerable pressure to rigorously control sea lice in farmed populations in order to protect wild salmonid stocks. However, to determine if there is actual benefit to the wild salmonid populations being obtained, scientific evidence for a cause–effect relationship should be available, particularly where such programs have existed for a length of time (see Heuch et al. 2005). This evidence is currently lacking. It is notable that support for such a relationship is not obtained from a risk analysis consideration of the several different correlations between data sets that have been used as evidence for a farm-associated impact (McVicar 2004).

RISK OF INTRODUCTION OF NEW (EXOTIC) PATHOGENS

It is universally recognized that the introduction of new infectious agents into an area previously free of that infection can lead to serious outbreaks of disease (Olivier, 2002; Kent 1994; Noakes et al. 2000). This is usually due to the lack of an evolved resistance in the indigenous populations that may act as susceptible hosts. Such events have been documented in human and animal populations and they also occur with fish. For example, an almost total destruction of Atlantic salmon populations in approximately 40 rivers in the west of Norway followed the accidental introduction of the skin fluke, *Gyrodactylus salaris*, from the Baltic areas in the 1980s. These Norwegian stocks of Atlantic salmon had no natural resistance to the infection while the Baltic strains of salmon populations were tolerant of the infection. More recently, the same parasite has been transferred into a White Sea draining river of Northern Finland and Russia (Rumjantzev and Ieshko 1997). This disaster has been the subject of intensive studies in affected countries (e.g., Koski and Heinimaa 2002; Dalgaard et al. 2003) and in Norway attempts to remove infection from affected rivers has involved the draconian measure of using rotenone to remove all fish capable of harboring the infection, not always with success (Johnsen and Jensen 1991; Mo 1996). Similarly, different strains of chinook, coho and steelhead have been shown to vary greatly in their resistance to the myxozoan parasite, *Ceratomyxa shasta*. Buchanan et al. (1983) and Ching and Parker (1989) demonstrated that chinook salmon from enzootic waters were far more resistant than strains from waters where the parasite is absent. Such examples illustrate well the desirability to avoid the introduction of new infection(s) capable of causing serious disease to a local fish population previously unexposed to it.

Treatments are both expensive and potentially damaging in farm populations. Even when suitable treatments are available, as with *G. salaris*, these are normally considered impractical when an infection is established in wild populations. Little, if anything, can be done to prevent or restrict the natural spread of diseases associated with the normal movements of fish populations between areas or the natural extension of the ranges of areas. Furthermore, other influences such as those associated with climate change, cannot be controlled. Approaches to restricting spread of disease must therefore focus on human actions particularly where risks of transfer of infection of significance to fish are created by activities such as trade. The greatest danger of introducing new disease lies in the transfer of live fish and eggs from affected areas with live fish presenting the highest risk. For many pathogens and parasites, there is no known vertical transmission or egg association. In other cases, egg surface disinfection will reduce the risk of transferring pathogens. True vertical transmission has been demonstrated in only a few cases, as for example, *Renibacterium salmoninarum* (Evelyn et al. 1986a, b).

The World Trade Organization (WTO) has addressed the risk of transfer of diseases between countries on a global scale through their Sanitary and Phytosanitary (SPS) Agreement. This sets out the reasonable conditions that may be applied by member countries to restrict trade because of valid concerns about the spread of diseases into their respective countries. The WTO commissioned the Office International des Epizooties (OIE) to specify the conditions appropriate to trade in animals under SPS, and the Fish Disease Commission of OIE has developed the International Aquatic Animal Health Code (the Code) to meet these requirements (OIE 2004). This sets out a list of diseases that are notifiable to OIE and a list of diseases of international concern based on their severity in respect of environmental effects, socio-economics, human health, or trade implications. To have international standardization in the detection and diagnosis of these diseases, a Diagnostic Manual for Aquatic Animal Diseases (the Manual) was also produced for these diseases listed by OIE in the Code. Both the Code and the Manual are updated on a regular basis. This process does not prevent a country from taking reasonable and justified measures to protect the health of its stocks of aquatic animals when a risk is detected and where diseases are identified as being of concern to a country.

Canada was in the vanguard of countries to recognize the risk of disease transfer into previously clean areas early in the development of an aquaculture industry. In the 1970s the Fish Health Protection Regulations (FHPR) were developed under the Fisheries Act to provide the regulatory framework for strict fish health conditions that had to be met for importation of fish/eggs or their transfer within Canada. The direct consequences are that Canada has prevented the introduction of serious diseases that exist elsewhere in the world. Currently the FHPR are being updated in the form of a National Aquatic Animal Health Program (NAAHP) to introduce greater flexibility, increase rapidity in response to new situations, and to keep controls in pace with the constantly evolving international standards, to which Canada has committed to maintain. In 2001, the Department of Fisheries and Oceans together with the provinces and stakeholders finalized a National Code on Introductions and Transfers through the Canadian Council of Fisheries and Aquaculture Ministers. The basis of the Code is a scientific risk assessment on any proposed transfer or introduction of fish into fish habitat or into a fish-rearing facility. The transfer of diseases/pathogens is flagged as one of the key risk factors in the code. When an activity is identified as potentially carrying fish disease into

an uninfected area, appropriate measures will be required to reduce the level of risk to an acceptable level. Transfers will only be licensed if risks of negative impacts to local populations are considered minimal.

Consequently, management steps taken by Canada have controlled the risk of introducing new diseases and the spread of locally occurring diseases to new areas within the country has been kept as low as is practically possible. The effectiveness of these actions is reflected in the fact that there are no recorded examples in Canada of any non-native fish diseases of concern being introduced either into farms or the natural environment with introductions of live fish or eggs. Similar precautions to prevent spread of diseases to new areas have been introduced in the US (Amos et al. 2000). However, it is necessary for all with an interest in the health status of fish to maintain a continual vigilance of new conditions of concern and of potential risk activities, particularly through the NAAHP.

From an aquaculture perspective, making use of the innate differences in resistance in fish and shellfish to particular dangerous disease agents is attractive. Beacham and Evelyn (1992) have described the genetic component of resistance to certain diseases such as bacterial kidney disease. Similar work has been done for oysters (*Crassostrea virginica*) and their resistance to MSX disease (Bower and McGladdery 2003). In areas enzootic for a disease, appropriate selection and/or breeding of less susceptible hosts could assist the aquaculture industry. The principle has also been recognized as having potential use for enhancement of rainbow trout resistant to the whirling disease agent *Myxobolus cerebralis*. Since the trout population in certain rivers (e.g., the Madison River in Montana) has been significantly reduced due to whirling disease, breeding and outplanting of trout strains resistant to the parasite has been discussed. However, this topic is of concern from the standpoint of preserving genetic integrity of the native rainbow trout strains.

RISK OF ABNORMAL ELEVATION OF LEVELS OF EXISTING DISEASES

Associated with the general inability of farms to avoid sources of infection in the surrounding environment and the higher opportunity for pathogen transmission and disease development, the management of disease has become an important feature of fish farming. Although considerable progress has been made in the prevention and control of farmed fish diseases as indicated by Youngson et al. (1998), the management of viral and parasitic diseases, (e.g., ISA virus, IHN virus, sea lice) remains problematic. Although wild hosts in the surrounding environment are the source of most infections known to occur in fish farms in Canada, concern has been expressed that the presence, in a fish farm, of a higher level of a disease agent than would be found to occur naturally in an area could provide a focus of infection for local wild stocks.

It is recognized that fish sharing waters share the risk of disease, but this relationship is not necessarily proportional to the water being shared. An understanding of the dynamics of infection and of the persistence of disease is necessary before conclusions can be reached on the extent of any new risk being posed by the occurrence of disease in farms to local wild fish populations. As Stewart (1998) pointed out, infections among fish or any other animal do not become established simply or inevitably

because a potential host has collided with an infectious agent. Specificity for a select range of fish is common for many infectious agents, while different host species that are capable of becoming infected may show a natural range of susceptibility to the same infection. Even the same host under high stress conditions (e.g., in elevated temperatures, spawning) may show higher susceptibility to infection (Bernoth et al. 1997).

When the transfer of infection from a farm to wild fish does occur, the subsequent development of a disease problem in the wild fish population is not inevitable. The development of an overt disease has long been recognized to be a complex product of the interaction among the host (fish), pathogens, and the environment (Snieszko 1974), but this model has now been recognized to be an oversimplification (Smith 1997; Hedrick 1998). Further, Olivier (2002) pointed out that even when infected fish are present, this should not be automatically correlated with potential disease transfers between a cultured fish and a wild fish, or vice versa, as all of several strict criteria must be fulfilled. These include the occurrence and persistence of the infection in the source population, the availability of susceptible potential new hosts, the viability and concentration of the infectious organism in the environment, and the ability of the infection to affect the recipient population from individual fish infections. Rose et al. (1989) demonstrated that an infective dose of *Aeromonas salmonicida* was diluted to non-infective levels within a few meters from a farm cage undergoing a furunculosis outbreak.

These complexities in the interaction between the occurrence of infection in fish and the development of disease and the insufficiency of basic research have contributed in a major way to the uncertainties in the evaluation of the level of effect of diseases in fish farms on wild fish populations. In this context, the role of sea lice on farms has been extensively debated internationally, but a conclusion has not been reached in any country (McVicar 2004). Similarly, the impact of IHN virus on wild stocks of fish is an area that is poorly understood and requires more research. IHN virus has been detected in Pacific herring and other species of marine fish near netpen sites of farmed Atlantic salmon undergoing losses due to the virus (Kent et al. 1998; Traxler unpublished). These findings, however, have only been from apparently healthy fish and there are no reports of high losses of marine finfish near IHN positive farms. Genetic typing of IHN virus indicates that the strain of virus between farmed and wild stocks is the same, suggesting exchange of the virus between these stocks, but does not indicate the direction. Atlantic salmon first contact IHN virus in the marine environment since there has been no reported occurrence of IHN virus in freshwater Atlantic salmon hatcheries in British Columbia.

Due to the year-round presence of fish farms in the marine environment, pathogens such as the IHN virus in farmed BC Atlantic salmon are also present for periods longer than would be normal in the marine environment. While the presence of IHN in marine reservoirs has long been a topic of discussion, there have been only a few demonstrated isolations of the virus in marine fish (Traxler et al. 1997; Kent et al. 1998). It is therefore possible that the virus is transferred from farms undergoing outbreaks to nearby marine fish. While Kent and Poppe (1998a) have found that herring can be infected with the virus, another study by Kocan et al. (1997) found that Pacific herring were quite resistant when exposed to IHN virus. In general, there is limited information on the possibility of transfer of the virus to other species. Such transmission may be of

special concern especially during the juvenile stages of certain species. Further work on this topic is required.

Pacific salmonids have historically been exposed to the IHN virus and other enzootic pathogens and have adapted to them. For instance, stocks in many rivers, and almost all sockeye stocks, are exposed to the IHN virus early in their life history while still in the freshwater. When migrating past infected farms, the impact on the population by the infectious load shed by the farm must be assumed to be much reduced since the survivors of the freshwater exposure are likely to be resistant. However, experimental verification would be useful.

SOURCES OF INFECTION IN FISH FARMS

With appropriate safeguards in place to prevent the introduction of new diseases into an area, the only origin of disease on fish farms can be from the environment in the surrounding area. Farms using water containing stocks of wild fish without treatment can therefore act as sentinels of the infection occurring in the natural environment. This is reflected in international disease management standards such as the OIE Aquatic Animal Health Code, where emphasis is placed on the surveillance of farmed animals. The risk of infection occurring on a fish farm is likely to be directly correlated both to the level of infection in its source and to the extent of contact between that source and the farm.

The often-stated belief that disease episodes do not occur in wild fish populations should be treated with some caution. The absence of evidence of epizootics cannot be interpreted as evidence of their absence. As in any wild animal population, large numbers of different potential disease-causing agents can occur in any one species of fish. In comparison to fish farms where knowledge has been sought to support disease management measures, there is generally a low level of information available on diseases in wild fish populations because control in these is generally not possible. It is true that epizootics are only rarely recorded in wild fish populations, but this is unlikely to reflect the real situation:

- In many situations, even though observed, many fish kills are not properly investigated for an infectious cause at the time of the event.
- It is now well known that, due to the typically low level of infectious agent, carriers of infection without evidence of clinical disease are difficult to detect.
- As discussed by McVicar (1997b), disease occurrence and dead fish are difficult to detect in the sea, due both to the size and inaccessibility of the environment
- Selectively high predation on sick animals leads to their rapid removal and unavailability for sampling.

In Canadian waters, the protistan parasite *Ichthyophonus hoferi* has been stated to cause high mortalities in the herring (*Clupea harengus harengus*) populations of the Gulf of St. Lawrence and Bay of Fundy in the 1950s and 1960s (Sindermann 1958, 1966) and in European waters in the early 1990s, with dead fish only rarely being seen in confined waters (McVicar, 1999). On the west of Canada, *I. hoferi* has been reported in Pacific herring (*Clupea harengus pallasi*) and rockfish (*Sebastes* spp.) in coastal waters of western North America (Kocan et al. 1999; Kent et al. 2001; Jones and Dawe. 2002). Prevalence increased from 5% to 70% in 0- to 2-year-old Puget Sound herring respectively with no noted associated increase in mortality (Kocan et al. 1999). However,

clinical disease was associated with *I. hoferi* infections in adult chinook salmon (*Oncorhynchus tshawytscha*) migrating in the Yukon River (Kocan et al. 2004). Comparison of 18S rDNA sequences indicated that *I. hoferi* isolates from herring and chinook salmon were more similar to each other than to isolates from rockfish (Criscione et al. 2002). This heterogeneity among *I. hoferi* isolates may reflect trophic interactions among host species. These observations suggest that the impact of *I hoferi* on herring or rockfish populations in the northeast Pacific Ocean is negligible at present. Kent and Poppe (1998b) reported heavy infections of *I. hoferi* in seawater-reared Atlantic salmon smolts and suggested the infections were acquired by eating infected calanoid copepods. However, these observations are rare in British Columbia and the impact of this parasite on farmed stock is considered negligible.

It is well documented that IHN virus is rarely detected in Pacific salmon during their marine phase (Amos et al. 1989; Mulcahy et al. 1984; Traxler 1983). One reported finding occurred in returning adult sockeye salmon off the west coast of Vancouver Island with a carrier rate of 12% (Traxler et al. 1997). There are reports of losses in sockeye salmon smolts due to IHN infection in both fresh and salt water (Follett and Burton 1995; Meyers and Winton 1995). At this stage of development, sockeye salmon may have an increased susceptibility to infection by IHN virus. In freshwater, IHN virus is often found at high prevalences and in high titers in sockeye salmon at both extremes of their life cycle. Virus levels in asymptomatic carriers increase substantially during the maturation and spawning period (Mulcahy and Pascho 1996; Traxler et al. 1997). The infection levels in sockeye salmon fry vary considerably from year to year, but significant losses can occur during the alevin stage (Traxler and Rankin 1989).

ENTRY OF INFECTION INTO FISH FARMS

The potential ways for local diseases to enter farms are through water, or with food or equipment. The relative susceptibility to infection of fish under farmed conditions and in the wild is often the subject of discussion, but for the disease most intensively studied – namely furunculosis – this was not identified as a significant factor (Bernoth et al. 1997). For the disease ISA, several risks factors have been identified to explain its transfer and spread. Jarp and Karlsen (1997) concluded that proximity (i.e. within 5 Km) to slaughterhouses or processing plants that do not properly disinfect wastewater and proximity to ISA-positive sites were the greatest risk factors. The spread of ISA outbreaks in farmed salmon in Scotland in 1998 was through fish movements and other farm practices, but diffuse spread may have operated locally (Stagg et al. 2001). The source of the initial outbreak was not determined.

Cusack et al. (2002) suggested that an outbreak of *Piscirickettsia salmonis* in farmed Atlantic salmon in Nova Scotia may have originated from fresh and frozen whole fish processed in the same harbor as the farm.

Water

With the exception of those using treated or ground sources of water, fish farms populations are vulnerable to disease from naturally occurring infections that are transmitted through water. Ground sources of salt water protected from infection are only found in very special local conditions such as with the gravel banks in northern New

Brunswick and in the Icelandic lava fields. Treatment of limited amounts of seawater is undertaken in some Norwegian salmon smolt producing facilities to address problems with freshwater acidity, water temperatures and the risk of locally occurring diseases in seawater (such as infectious salmon anemia). Such treatments are impractical for the large volumes of water required for the commercial production of larger fish in mariculture and the transmission of infection from wild sources through water thus remains a major area of risk to marine fish farms. The entry of infection into waters of a fish farm by predators such as birds feeding on infected fish in other areas is theoretically possible (Price and Nickum 1995), but this has only been suggested in onshore tanks and ponds. It is more probable that the initiation of infections in marine fish farms is related to the level of infection in the surrounding environment, such as in wild fish, and the proximity of these to fish farms. From the Norwegian experience with ISA, it is clear that even onshore farms are still vulnerable to infections from untreated seawater, although the risk from some parasites, such as sea lice may be reduced.

Food

During the early stages of salmonid farming in the sea in Europe, disease outbreaks due to bacterial infections (e.g., *Vibrio* species) and parasites (e.g., *Ichthyophonus*) were directly attributed to the use of fresh fish as a main source of food. However, in current Canadian mariculture, the exclusive use of manufactured feeds through which processing destroys known infections of concern has removed this source of disease. In addition, the conditioning of farmed fish to manufactured food pellets and the provision of adequate levels of feeding discourages farmed fish foraging on wild sources of food within cages. As seen in regular surveys of farmed salmon by the Scottish Fishery Research Services, the occurrence in salmonids of infections such as the roundworm *Anisakis simplex*, which is of public health importance, now only occurs in wild fish through their feeding on infected wild fish and crustaceans.

Equipment

Although farm gear, including nets, graders, harvesting equipment, and even staff boots and clothing, can potentially transfer bacterial and viral infection between farms, the level of infection present on farms is usually sufficiently low for this to be considered a low-risk area. It is only in epizootic disease situations that particular caution has to be taken and good farm management practices in relation to biosecurity measures can be effective in both further reducing the level of risk and in being precautionary against possible future disease incidents.

Level of Infection on Farms

The conditions typically found within a fish farm, such as crowding of fish, are such that once infection is present there is a risk of the spread of the infection and the development of disease outbreaks. In this respect, fish farming is no different from intensive or semi-intensive farming on land. Disease thus remains one of the major and unpredictable risk areas of fish farming. However, as Youngson et al. (1998) noted, the development of effective vaccines in the fish farming industry has significantly reduced the problems with some of the serious diseases. These have been available longest and

are most effective for some bacterial diseases such as vibriosis and furunculosis, but are also now commercially available for the viral diseases IPN and ISA. Where there are risks of disease outbreaks and effective vaccines are not available, alternative disease management approaches including removing all fish from a farm facility to break disease cycles, area or bay management, and use of single generations and targeted administration of chemotherapeutants at critical times in disease development cycles (e.g., of lice) have proved to be highly successful in reducing disease incidents on farms (McVicar 2004).

The serious potential implication of disease on a fish farm means that it is in the interest of the fish farmer to maintain the level of any outbreaks as low as possible. As profit margins in marine fish farming have narrowed in the last few years, the urgency in achieving high levels of survival has increased. This is not to say that all disease outbreaks are prevented as has been evident with the outbreaks of ISA in New Brunswick and of infectious hematopoetic necrosis (IHN) in British Columbia. In such cases, voluntary and provincial cooperative management programs have been introduced to reduce the level of disease. During such incidents, the level of infectious agent present on a farm clearly increases as does the level of shedding into the surrounding waters.

Transfer from Wild Fish to Farms

As mentioned previously, there is no evidence that diseases in fish farms have affected wild marine populations (Olivier 2002). On the contrary, most of the scientific evidence accumulated indicates wild fish can act as reservoirs and if conditions permit can infect fish farms. Sockeye salmon are a suspected source of IHN virus causing infection in marine netpens because of the finding of the virus in fish in the marine environment. However, there could be a yet unidentified source which also infects sockeye salmon in the marine environment (Traxler et al. 1997). A major phylogenetic analysis of IHN virus isolates from North America demonstrated that there was little genetic diversity in IHN virus isolates from Alaska, British Columbia and coastal Washington (Kurath et al. 2003). Many salmon populations from this large geographic region have overlapping ocean migrations and this co-mingling of populations could result in virus transmission between stocks or from other undetermined hosts or reservoirs, thus helping to maintain homogeneity among IHN virus in this large area.

Several species of sea lice (*Lepeophtheirus* spp., *Caligus* spp.) occur naturally on wild fishes along the coast of British Columbia (Margolis and Arthur 1979; McDonald and Margolis 1995). While the taxonomic diversity of sea lice in coastal British Columbia has been well documented, very little is known about the epizootiology of sea lice among Pacific salmon, particularly concerning transmission to juveniles in inshore waters. Consequently, although we know that netpen-reared Atlantic salmon smolts in newly stocked areas initially acquire infections from wild sources, the relative contribution of subsequent infections that are derived from wild salmon and farmed salmon sources has not been defined. Anecdotal information suggests that increasing levels of lice on farmed salmon coincide with migrations of adult pink salmon adjacent to the farms.

Risk of Transmission to Wild Fish

Diseases may be transmitted in water, generally for short distances, through the escape of infected animals or through direct contact with an infection source (infected animal or other contaminated material). However, the level of risk will vary considerably with different infectious agents. Because of the complexity of factors influencing the initiation of infection and thereafter the development of disease, the simplistic view of risk being directly related to the level of exposure is not tenable. For transfer of significant infection between farmed and wild fish, Olivier (2002) detailed a set of criteria that must be fulfilled in their entirety. These include a source of the pathogen, the persistence of the pathogen in a viable state and at an infectious level, the presence of a susceptible host, and the presence of enough susceptible hosts to transfer infection between them to initiate infection in a population. Disease may be spread between wild and cultured fish through migration of wild fish near or close to an infected fish farm or cage, or through the escape of infected cultured fish. Olivier (2002) concluded there was no documented evidence to substantiate the hypothesis that wild Atlantic salmon populations were declining in the Atlantic provinces of Canada as a result of spread of diseases originating from farmed fish.

Olivier (2002) noted that although disease interactions between wild and cultured fish do occur, the effect of these transfers on either wild or cultured fish could not be easily quantified. Stewart (1998) reviewed available information on the spread through water of different diseases of importance to Atlantic salmon and concluded that in relation to the movement of waters in the Passamaquoddy Bay Region of New Brunswick that distances of 1 km were not effective barriers to the spread of disease. In some cases, even longer distances were not considered proof against the transmission of disease, and where vectors were included there were no specific practical distances that could be delineated.

Attempts have been made to evaluate the risk of spread of disease as a function of distance from fish farms from a theoretical point of view (e.g., Turrell and Munro, 1988), but qualitative analysis based on practical experiences of risk of interaction of disease between farms can provide realistic data. However, it is important to note that these data are relevant only to the specific area and disease for which they have been compiled. Using this approach, Norwegian authorities established "combat zones" around infected farms and in accordance with the OIE Aquatic Animal Health Code, and the Scottish authorities established infected and surveillance zones around ISA infected foci.

Information on waterborne dispersion of material, including disease agents, at individual farms will require detailed studies. Tracers such as compounds associated with fish fecal matter have been suggested to study dispersion of material from farms (Hargrave 2003). This information will assist in gaining knowledge on significant pathogen dispersal rates from farms affected by a disease since pathogens are frequently shed with feces. An alternative approach of assessing risk to wild fish populations is to measure the spread of infective stages out from an infected farm source. In Ireland, the dispersion pattern of the planktonic larval infective stages of salmon lice from an infected fish farm was researched by Costelloe et al. (1998). The distribution of larval lice from a farm population was found to be dependent on the release of the larvae from the cages and subsequently on the water currents of the area. A high retention of larvae within cages was detected and of those present in the external water body, a 90% reduction in

larval densities was found within 1 km of the farm. The highest levels of larval lice found occurred sporadically close to the mouth of a river, but distant from the infected farm, presenting the conclusion these were derived from wild salmonids either resident or migrating into the area. Detection of the dispersion of bacterial and viral particles would be even more technically difficult.

The escape of diseased fish from fish farms constitutes a risk that infection will be transferred from the immediate vicinity of the farms into the wider environment. However, the direct determination of the effects of disease in wild fish populations, particularly in the large marine environment, is difficult. As pointed out by McVicar (1997b), sick fish that show any abnormal behavior are likely to be rapidly removed from the area by predators and any random samples of fish taken will almost inevitably show only healthy animals, those with asymptomatic infection levels or those with benign types of disease. Work done with Atlantic salmon escapes in Norway indicates that high proportions of farmed salmon were found only in rivers having farms situated within 20 km from the outlet (Gausen and Moen 1991). Studies done with intentional releases of domesticated chinook salmon in BC (Kreiberg et al. 1989) show that returns are generally low. This low return is thought to reflect changes in oceanographic conditions and the rate is similar to the releases from enhancement facilities. Migratory patterns are those of natural stocks. In general, the return indicates that should fish carrying an enzootic disease agent be released, the disease is not likely to be spread to distant areas. Hence, strains of diseases that may be present in an area are not likely to be transferred out of the area.

The initial level of the risk of infection problems in wild fish being associated with escaped farmed fish is dependent on the same list of criteria listed by Olivier (2002). Particularly important are the length of survival and the behavior of the escaped fish after leaving a farm and the reduced disease transmission opportunity in the lower fish densities outside the farm. Jacobsen et al. (1992) found that farmed Atlantic salmon may stay in the vicinity of the site of escape for up to 3 weeks and Hansen et al. (1993) have shown that substantial numbers of escaped salmon can survive and appear on open ocean feeding grounds. However, farmed fish in general are recognized to be maladapted to survival in the wild (Fleming et al. 2000). Any survivors of escaped farmed fish in the wild are therefore likely to be only the fittest. In the present context, the additional liability of fish carrying disease when they escape is likely to result in the early disappearance of the most seriously affected fish. These are the most likely candidates for onward transmission of infection at levels greater than concomitant natural sources. The significance of the risk associated with diseased fish escaping from farms is therefore likely to be rapidly reduced towards levels equivalent to that for wild fish.

Jacobsen and Gard (1997) found that the prevalence and abundance of salmon lice on one sea winter Atlantic salmon were significantly higher on escaped farmed fish than on wild salmon. Possible explanations suggested for this difference were an increased residence time in coastal waters of escaped farm fish prior to their migration to the open ocean, and the greater tolerance to infection because of the larger size of fish at the time of their escape, compared with wild smolts. This difference disappeared during the following year while the salmon were at sea. The numbers of these fish and such behavioral differences will result in the transfer of additional levels of lice from coastal

areas into the oceanic feeding grounds, although offset against this is the reduced stock sizes of wild salmon. Other disease conditions are likely to follow the same pattern.

RISK OF ABNORMAL DISTRIBUTION OF DISEASE

SEASON AND LOCATION

There is a belief that fish farms may provide a unique or abnormal focus of infection at times of the year, or in areas not normally found with natural patterns of infection. Current evidence indicates that the diseases currently occurring in fish farms in Canada have been obtained from local wild sources, and as transfer of infection requires the presence of susceptible fish in the surrounding environment, the potential significance of this as an issue is limited. Any transfer of infection from farms to a group of wild fish that would otherwise be uninfected, such as the smolts of salmonids, or an abnormally high level of infection would constitute a new risk. However, if there is a concurrent natural infection occurring in the area, the new level of the risk would then be proportional to that.

The continuing IHN epizootics of farmed Atlantic salmon have resulted in release of the virus at times when young salmonids and non-salmonids may be present around fish farms. This could result in an undetermined risk of viral infection to these fish. Additional research on susceptibility studies of young marine fish is required to answer many of these questions.

The major discussion in this area has been the risk to newly migrating smolts from salmon lice infections with a source in fish farms. As indicated above, despite intensive research efforts in this area, there has been no international resolution on the extent and consequences of this or of the natural contribution from other salmonids in the area. There has been a lack of information on the occurrence of sea lice on juvenile salmonid or non-salmonid fishes in the northeast Pacific Ocean. Parker and Margolis (1964) reported the impact of *Caligus clemensi* on juvenile pink salmon (*Oncorhynchus gorbuscha*) on the central coast of British Columbia. Anadromous *Oncorhynchus* species return to coastal waters and enter their natal streams in British Columbia from June through December depending on species and stock. Similarly, juveniles migrate into the marine environment between March and July. This general lack of coincidence between the migrations of adult and juvenile salmon through inshore waters suggests that infections on returning adult salmon may not contribute significantly to infections on outmigrating juveniles. Very little is known about the natural transmission of sea lice to juvenile salmon in coastal waters of British Columbia. To rectify this, DFO conducted a surveillance program of juvenile *Oncorhynchus* spp. between March and June of 2003 in the Broughton Archipelago region of coastal BC. This systematic collection by beach and purse seine monitored the distribution and abundance of salmon and the prevalence and intensity of their sea lice over a 15-week period. Observations from this survey indicate that juvenile pink and chum salmon are infected with *Caligus* sp. and *Lepeophtheirus* sp. very shortly after they enter the marine environment and that the prevalence of infection increases with time (Jones and Nemec 2004). Other observations indicate that some chinook and coho salmon overwinter in coastal waters, including the Broughton

Archipelago, and the finding of lice on these fish indicated that they contribute to the reservoir of infection for outmigrating juveniles (Trudel and Jones unpublished). As previously indicated, neither Olivier (2002) nor McVicar (2004) were able to document evidence that diseases from farmed fish had contributed to declines in salmonid populations, despite there being extensive research into this topic. However, the lack of data currently available should not preclude further research into this area.

CONCLUSIONS

Currently, it is accepted that there is a two-way transfer of infectious agents between wild fish and farms, but there is no evidence available in Canada indicating a risk of infections from farms causing adverse effects on the viability of wild fish populations.

The greatest disease risk to both farmed and wild populations of fish in Canadian marine waters lies in the possibility of an introduction of an exotic pathogen to which local fish stocks have a high susceptibility to infection and a low resistance to prevent the occurrence of a disease incident. It is essential that a strong guard should continue to be maintained through compliance with effective regulations to prevent diseases of significance to Canada being introduced. These measures should equally apply to relocation of materials carrying risk of transfer of viable infective agents that pose a new serious risk from infected areas abroad as well as other areas within Canada.

For both wild and farmed fish stocks, it is necessary to specify diseases of concern to all or parts of Canada and classify them as reportable to meet national and international disease control regulations. Contingency plans based on risk analysis should be developed for exotic diseases and uncontrollable disease outbreaks to enable the rapid implementation of disease management actions, including best husbandry practices on farms. Currently, these requirements are being integrated into a comprehensive revision of Canadian aquatic animal health management through the development of a National Aquatic Animal Health Program (NAAHP), which is built on a collaborative partnership among federal, provincial, industry, and other stakeholders in sustainable seafood productivity. Similarly, international cooperation is ongoing to address international trade and trans-boundary issues related to effective aquatic animal health management. As increased effort is put into wild and cultured resource surveillance, new findings are bound to emerge. This will require timely and targeted research to effectively distinguish the infective agents that pose a real risk to farmed and wild resources from those that exist in relative harmony with their hosts.

RECOMMENDED RESEARCH

- Upon identification of new disease hazards, directed research based on the principles of risk assessment must be conducted to provide options for their effective management in a structured manner.

- To better understand epizootics, there is a requirement to make better use of mathematical models including environmental an well as biological data

- Baseline information on the disease status of wild stocks or a newly cultured species, prior to the development of aquaculture in an area and with emphasis on temporal and spatial variation would facilitate understanding of any effects that may be attributed to aquaculture.

- When a new species susceptible to a disease enzootic in native stocks is cultured, baseline information is desirable on pathogenicity and on wild–farmed fish disease interactions e.g., nodaviruses in the family *Betanoviridae*. Studies on strain variations and susceptibility to infection and disease should be included.

- More information is needed on the cause–effect relationship in the transmission of disease between wild and cultured fish. For example, before meaningful comment can be made on the significance of any correlations found between data on disease occurrence in both situations, knowledge is required of the range of factors affecting transmission of infection and the establishment of disease such as those listed by Bernoth et al. (1997) for furunculosis.

- Further studies are needed to evaluate whether sea lice transfer between wild and cultured fish has any direct negative effect on the overall health of wild populations, particularly on the epizootiology of sea lice among Pacific salmon and its transmission to juveniles in inshore waters. Consideration should be given to mechanisms that control lice on farms in relation to infections being derived from wild reservoirs.

- Faster, more sensitive diagnostic tests for IHN are needed and the factors involved in transmission and outbreaks in other fish species determined. Awareness of key epizootiological information on IHN needs to be developed to improve the speed of diagnosis and the effectiveness of management measures.

- More research is needed to understand the life cycles of marine myxozoa, such as *Kudoa thyrsites* and *P. minibicornis*, to develop effective prevention and control strategies.

- Studies on waterborne disease agents or infective stages are needed to determine pathogen dispersion rates from infected fish.

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TROPHIC INTERACTIONS BETWEEN FINFISH AQUACULTURE AND WILD MARINE FISH

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EXECUTIVE SUMMARY

This review examines the literature on trophic interactions between marine finfish aquaculture and wild fish populations to determine the state of existing knowledge and identify research gaps for future study. Three questions are central to this discussion: What is the predation effect of caged finfish on wild fish and available prey? Do finfish farm sites attract wild fish and affect their productivity? What are the competition and predation effects of escaped finfish on local and regional wild fish populations?

Recent aquaculture reviews have highlighted ecosystem effects and provided general discussion on farm site attraction and the predation and competition effects of caged and escaped finfish. However, no comprehensive reviews exist. The majority of studies on these topics have focused on behavioural and genetic interactions between escaped finfish and wild fish, or on the attraction of wild fish to farm sites. Little direct empirical or experimental work has been conducted to address these questions and a knowledge gap exists in northern temperate marine systems, including Canada.

The published literature does indicate that cultured finfish can have measurable effects through predation of, attraction to, and competition with wild fish or available wild prey. These effects can occur at the level of local farm sites and ecosystems, and can occur potentially at regional scales. While these effects vary with respect to the three questions above, they are generally linked by the nature and productivity of the local ecosystem around farm sites (i.e. warm oligotrophic to eutrophic; cool oligotrophic to eutrophic), the number and species of cultured finfish, and the number and proximity of farm sites in relation to concentrations of wild fish. Available literature on these subjects is limited and therefore it is difficult to quantify the relevance and risk of effects resulting from trophic level interactions between farmed finfish and wild fish populations.

Only a few studies have examined the predation effects of caged finfish on wild fish, and those completed to date have been conducted in marine systems in British Columbia. Results indicate that caged salmon feed at low rates on wild fish and plankton prey and that this interaction is dependent on the salmon species cultured, season, and farm location. Farmed fish consumed low numbers of wild fish and plankton but showed trends in behaviour and prey selection similar to those of wild salmon. The studies were

observational in nature and did not fully test the effects of caged salmon feeding on wild prey. Future Canadian studies should incorporate an experimental design to evaluate the predation effects of caged finfish on wild fish and prey, and determine the variation in potential effects among caged finfish species, season, and spatial proximity of farm sites to wild fish populations.

A few studies have been conducted in northern temperate marine systems to examine the attraction of wild fish to farm sites. Results indicate that wild fish use farm sites as artificial reefs or shelter, as well as enhanced sources of food from surplus pellet feed, farm and fish waste, and from the abundance of local macrofauna on or near these sites. Results also indicate that wild fish densities increase by 1- to 10-fold near cool northern temperate farm sites as a result of local attraction, but show little response in overall wild fish community biodiversity. Increases in density, population size and age structure, and overall community biodiversity near warmer nutrient-poor farm sites indicates higher levels of attraction response by wild fish. Further study is needed in Canada to examine the wild fish population and community level attraction to farm sites and determine what level of interaction exists. These studies should consider use of appropriate indicator species to determine levels of interactions.

Limited data exist on the number, local distribution, and feeding behaviour of escaped farmed fish and their potential interactions with wild fish. New study is needed to quantify potential interactions and effects of escaped farm fish on wild fish populations. The existing literature shows three patterns of interaction. High densities of escaped fish are negatively associated with the abundance and diversity of wild fish, and escaped fish are principally competitors and secondarily predators. Lower densities of locally escaped farmed fish have inconclusive effects on wild fish; although escaped fish do revert to wild-type feeding behaviour. Finally, exotic, as compared with endemic, farmed species show differences in feeding behaviour. There is a knowledge gap in available research linking escaped fish density, survival and feeding to wild fish populations in proximity to farm sites.

This state of knowledge should be integrated into an overall appraisal of the risks of farmed finfish on wild fish populations from other reviews to prioritize research and develop novel management approaches.

GAPS IN KNOWLEDGE

1. *New studies are required to determine whether caged marine finfish (salmon and other cultured fish species like sablefish, cod, halibut) feed on local wild populations of plankton and fish. These studies should examine local and regional scales of influence between farmed finfish and wild fish populations to determine the relevance of this interaction.*
2. *New studies are required to determine the level and type of attraction by wild fish to marine finfish farm sites in Canada.*

3. *Studies of farmed finfish escaped into natural environments are required to link cause and consequences for wild fish and their ecosystems at both local and regional scales.*
4. *Comprehensive monitoring and incident reporting are required to clearly establish the timing, quantities, species and condition of escaped farmed fish into the wild.*
5. *Most study results to date have incorporated little experimental design and have been empirical or observational in nature. Experimental or adaptive approaches should be considered to provide a range of risk exposure of finfish aquaculture to wild fish populations to reflect growing experience and understanding.*
6. *New study is required to compare and contrast the diet and consumption patterns of caged, escaped and wild salmon with the distribution of available food organisms and environmental conditions in marine environments.*
7. *The selection of research priorities for study of farmed fish and wild fish interactions should be based on the levels of perceived risk to wild fish populations and local ecosystems. The objective of this research should be to evaluate and quantify the risk.*

INTERACTIONS TROPHIQUES ENTRE LES POISSONS MARINS SAUVAGES ET D'ÉLEVAGE

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SOMMAIRE

La présente revue de la littérature porte sur les interactions trophiques entre les poissons marins d'élevage et les populations de poissons sauvages afin de déterminer l'état des connaissances sur le sujet et de cerner les lacunes à combler en matière de recherche. Trois questions sont au cœur des discussions sur le sujet : Quel est l'effet de la prédation par les poissons en cage sur les poissons sauvages et les proies disponibles? Est-ce que les sites d'élevage attirent les poissons sauvages et ont-ils une incidence sur la productivité de ceux-ci? Quels sont les effets de la prédation et de la concurrence par les poissons d'élevage évadés sur les populations de poissons sauvages locales et régionales?

De récents examens de l'aquaculture ont mis en évidence les effets de cette activité sur les écosystèmes et ont traité de façon générale de l'attrait que les sites d'élevage exercent sur les poissons sauvages ainsi que des effets de la prédation et de la concurrence par les poissons en cage et ceux qui s'en évadent. Aucun examen détaillé n'a toutefois été réalisé sur le sujet. La majorité des études a porté sur les interactions génétiques et comportementales entre les évadés et les poissons sauvages, ou encore sur l'attrait qu'exercent les sites d'élevage sur les poissons sauvages. Peu de travaux empiriques ou expérimentaux directs ont été effectués afin d'aborder ces questions, et il existe une lacune dans les connaissances sur les écosystèmes marins tempérés du Nord, y compris ceux au Canada.

La littérature indique que les poissons d'élevage peuvent avoir des effets mesurables sur les poissons sauvages ou les proies sauvages disponibles par le biais de la prédation, de la concurrence et de l'attraction. Ces effets peuvent survenir à l'échelle locale (sites d'élevage et écosystèmes) et, potentiellement, à l'échelle régionale. Bien que ces effets varient en ce qui concerne les trois questions susmentionnées, ils sont généralement interreliés par le biais de la nature et de la productivité de l'écosystème environnant (c.-à-d. conditions chaudes et milieu oligotrophe à eutrophe; conditions fraîches et milieu oligotrophe à eutrophe), du nombre de poissons d'élevage, des espèces concernées, du nombre de sites d'élevage et de la distance de ceux-ci par rapport aux concentrations de poissons sauvages. Il n'existe qu'un nombre limité de documents disponibles sur ces sujets, et il est par conséquent difficile de quantifier la pertinence et le risque associés aux conséquences des interactions trophiques entre les poissons d'élevage et les populations de poissons sauvages.

Trophic interactions between finfish aquaculture and wild marine fish

Seules quelques études ont porté sur les effets de la prédation par les poissons en cage sur les poissons sauvages, et celles terminées à ce jour ont été effectuées dans des écosystèmes marins en Colombie-Britannique. Les résultats de ces études indiquent que les saumons en cage consomment peu de poissons sauvages et de plancton et que cette interaction varie en fonction des espèces de saumon élevées, de la saison et du site d'élevage. Les poissons d'élevage consomment peu de poissons sauvages et de plancton, mais leur comportement et leur choix de proies sont semblables à ceux des poissons sauvages. Les études reposaient sur des observations et n'ont pas examiné en profondeur les effets de la prédation par les saumons en cage sur les proies sauvages. Les études qui seront menées ultérieurement au Canada devraient comprendre un modèle expérimental afin d'évaluer les effets de la prédation par les poissons en cage sur les poissons et les proies sauvages ainsi que de déterminer la variation des effets potentiels en fonction des espèces en cage, de la saison et de la distance entre les sites d'élevage et les populations de poissons sauvages.

Quelques études ont été menées dans des écosystèmes marins tempérés du Nord afin d'examiner l'attrait que les sites d'élevage exercent sur les poissons sauvages. Les résultats de ces études indiquent que les poissons sauvages utilisent les sites d'élevage comme récifs ou abris artificiels et que ces sites constituent un lieu d'alimentation de prédilection en raison de l'excédent de granules de nourriture, des déchets organiques des fermes et de l'abondante macrofaune présente sur place ou à proximité. Les résultats indiquent également que les densités de poissons sauvages sont de une à dix fois plus élevées près des sites d'élevage en milieu nordique tempéré et frais en raison de l'attraction à l'échelle locale, mais que la biodiversité globale des communautés de poissons sauvages varie peu à ces sites. Les hausses sur le plan de la densité, de la taille des populations, de la structure d'âge et de la biodiversité globale des communautés à proximité des sites d'élevage en milieux pauvres en éléments nutritifs et aux conditions plus chaudes indiquent qu'un nombre plus élevé de poissons sauvages sont attirés par ces sites. D'autres études sont nécessaires au Canada afin d'examiner l'attrait qu'exercent les sites d'élevage sur les populations et les communautés de poissons sauvages et de déterminer les degrés d'interaction. Ces études devraient comprendre l'utilisation d'espèces indicatrices appropriées pour déterminer les degrés d'interaction.

Il existe une quantité limitée de données sur le nombre, la répartition à l'échelle locale et le comportement d'alimentation des poissons d'élevage évadés ainsi que sur leurs interactions possibles avec les poissons sauvages. De nouvelles études sont nécessaires pour quantifier les interactions possibles entre les évadés et les populations de poissons sauvages ainsi que les effets potentiels des évadés sur celles-ci. La littérature montre trois types d'interactions possibles. Les densités élevées d'évadés sont associées négativement à l'abondance et à la diversité des poissons sauvages, et les évadés sont d'abord des concurrents et ensuite des prédateurs. Les densités faibles d'évadés ont des effets non concluants sur les poissons sauvages, mais les évadés adoptent un comportement d'alimentation semblable à celui des poissons sauvages. Finalement, les espèces d'élevage exotiques, par opposition aux espèces d'élevage indigènes, montrent des différences sur le plan du comportement d'alimentation. Il existe une lacune dans les

connaissances sur la relation entre la densité, la survie et l'alimentation des évadés et les populations de poissons sauvages à proximité des sites d'élevage.

Cet état des connaissances devrait être intégré à une évaluation globale des risques que présentent les poissons d'élevage pour les populations de poissons sauvages (résultats des examens antérieurs) afin d'établir les priorités en matière de recherche et d'élaborer de nouvelles approches de gestion.

LACUNES DANS LES CONNAISSANCES

1. *De nouvelles études sont nécessaires afin de déterminer si les poissons marins en cage (saumon et autres espèces de poissons d'élevage, telles la morue charbonnière, la morue et le flétan) se nourrissent de poissons sauvages de populations locales et de plancton. Ces études devraient examiner l'échelle d'influence locale et régionale entre les poissons d'élevage et les populations de poissons sauvages afin de déterminer la pertinence de cette interaction.*
2. *De nouvelles études sont nécessaires afin de déterminer le degré et le type d'attraction qu'exercent les sites d'élevage de poissons marins sur les poissons sauvages au Canada.*
3. *Des études sur les évasions de poissons d'élevage sont nécessaires afin d'établir des relations entre les causes des évasions et leurs effets, à l'échelle locale et régionale, sur les poissons sauvages et leur écosystème.*
4. *Une surveillance attentive et la préparation de rapports d'incident sont nécessaires pour établir clairement le moment des évasions, le nombre d'évadés, les espèces concernées et l'état des évadés.*
5. *La plupart des études menées à ce jour ont été de nature empirique ou ont reposé sur des observations et n'ont comporté que peu d'expériences. Des approches expérimentales ou adaptatives devraient être prises en considération afin de soumettre des populations de poissons sauvages à une gamme de niveaux d'exposition au risque lié aux poissons d'élevage de manière à tenir compte de l'évolution des connaissances.*
6. *Une nouvelle étude est nécessaire afin de comparer le régime alimentaire et les habitudes de consommation des saumons en cage, évadés et sauvages en fonction de la distribution des proies disponibles et des conditions dans le milieu marin.*
7. *Le choix des priorités de recherche aux fins d'étude des interactions entre les poissons sauvages et les poissons d'élevage devrait être fondé sur le niveau de risque perçu pour les populations de poissons sauvages et les écosystèmes locaux. L'objectif de cette recherche devrait être d'évaluer et de quantifier le risque.*

INTRODUCTION

This review examines literature on trophic interactions between farmed marine finfish and wild fish populations to determine the state of existing knowledge and to identify research gaps for future study. In a recent review on aquaculture, Hargrave (2003) describes three categories of effects of finfish aquaculture on local marine ecosystems: eutrophication, sedimentation and food web structure and function. This paper expands Hargrave's discussion of effects on food web structure and function with a focus on three specific areas of trophic interactions between farmed fish and wild marine fish populations: (a) predation effects of caged fish on wild marine fish and plankton entering fish farm cages, (b) attraction and potential production increases of wild fish and plankton near farm sites, and (c) resource competition with and predation on wild marine fish by escaped farm fish.

LITERATURE REVIEW

A literature review has been compiled through key word and key phrase searches of multiple sources, resulting in the following hierarchy of records by topic used in this discussion (as of 31 December 2005):

- 5300 total records on aquaculture;
- 4809 records on various aspects of fish farms and finfish mariculture;
- 4196 records on salmon or marine fish aquaculture;
- 931 records related to "net pens", "cage" and "salmon, marine and farm", but involved various aspects of finfish aquaculture including feed delivery systems, sea lice, site selection, quality control, diseases, ecosystem and environmental issues associated with farm site operation and location, nutrient loading, wild fish, cage-reared fish impacts and fish farm escapes;
- 154 records related to trophic (or ecosystem) interactions of farmed fish with their natural environments:
  - 79 records related to trophic interactions of farmed fish with wild fish;
  - 30 records on attraction and feeding of wild fish in proximity to fish farm;
  - 25 records on farmed fish feeding within cages and as escaped fish in the wild;
  - 15 records on escaped farmed fish feeding in the wild; and
  - 10 records on farmed fish still caged, feeding on wild fish or prey.

This literature review reveals several sources of uncertainty. The database provided a representative, rather than exhaustive, compilation of information and literature sources, so that the state of knowledge was potentially under-represented. Multiple search engines were used to explore and retrieve literature from various collections, however the full extent of literature on the trophic interactions of farmed finfish and wild fish remains fully unknown. These results underscore the fact that few published studies exist on the topic of interactions between farmed fish and wild fish populations.

PRESENT KNOWLEDGE

High value finfish marine aquaculture in British Columbia and in the Maritime provinces of Canada has developed rapidly in part as a result of the decline in harvests of commercially and economically viable wild fish populations, particularly salmon and sablefish in British Columbia (BC) and salmon and cod in the Maritimes. This rapid development has led to general concerns about the effects of aquaculture on wild fish. In BC, direct predation by caged salmon on locally distributed or migrating juvenile anadromous salmonids is one explanation for large variations in wild salmon abundance (Black et al. 1992). Salmon from streams that originate near high densities of fish farm operations are considered most affected (Gausen and Moen 1991; PFRCC 2002). It has also been suggested that salmon aquaculture facilities have disrupted historic migration corridors of commercially viable fish species along coastlines and thereby contributed to declines of local traditional trap fisheries (herring, lobster, scallops, cod, pollock and haddock) in Canada's Bay of Fundy (Stephenson 1990).

Global farmed salmon and other marine finfish production has risen from approximately 500,000 metric tons during the 1990s to over 1.2 million metric tons in the last 5 years (ICES 2005b). In 2004 farmed salmon production was distributed among Norway 44%, Chile 23%, Scotland 15%, British Columbia 6%, Faroes 4% and Atlantic Canada 3%. On the Pacific coast, Canadian marine finfish aquaculture is concentrated around the fjords and inlets of northern Vancouver Island and the central coast, and in Atlantic Canada in New Brunswick and Nova Scotia in the Bay of Fundy and, more recently, along the eastern coast of Newfoundland. The continued growth of cage-farmed marine fish in Canada has raised concern about the potential effects of farmed fish on wild fish populations.

This report reviews three areas of interaction between farmed fish and wild marine fish: (a) direct predation by caged farm fish on wild fish and plankton; (b) attraction of wild fish and plankton populations to farm sites; and (c) predatory and competitive effects of escaped farmed fish on wild fish populations in marine ecosystems. This report does not examine other potential trophic interactions between farmed fish and the environment such as those associated with the genetic and behavioural interactions of escaped and wild fish in freshwater, the transfer of disease or parasites between farmed and wild fish or the use of wild fish supplies as protein sources for fish feed. These subjects are beyond the scope of this study and have been reviewed extensively in the Fisheries and Oceans Canada State of Knowledge (Fisheries and Oceans 2003) documents and other reviews including Pearson and Black (2001), Weir and Grant (2005), Naylor et al. 2000, and Tacon 2004. Aquaculture reviews that have omitted or had little comment on trophic level interactions between farmed fish and wild fish populations include: Black (2002), Fisheries and Oceans (2003), FWS/NOAA (2000), Gillespie (1986), Goldberg et al. (2001), Gross (1998), Hargrave (ed.) (2005), Heggeberget et al. (1993), Iwama (1991), Milewski (2001), Nash (2003), Pearson and Black (2001), Waknitz et al. (2003), Winsby et al. (1996), and Windsor (2000).

A. PREDATION EFFECTS ON WILD FISH

Increased production from aquaculture has raised specific concerns about potential trophic interactions and predation effects by piscivorous farm fish on sensitive or threatened wild fish populations. Marine aquaculture sites are often placed in coastal areas with the same properties that create viable and important wild fish habitats. In British Columbia, New Brunswick, Nova Scotia, and Newfoundland, many species of wild fish (salmon, herring etc). migrate to or originate from systems in close proximity to present fish farm sites (e.g. BC: see PFRCC 2002; NB, NS: see Ritter et al. 1999). Sheltered coastal areas used to site marine fish farm operations (Levings et al. 1995) are also important habitats for juvenile salmon, as well as migration corridors for locally important northern marine demersal and pelagic marine species (e.g., eulachon *Thaleichthys pacificus*, herring *Clupea harengus*, whiting *Gadus sp.*, saithe *Pollachius virens*). Salmon species used in Canadian aquaculture are primarily piscivorous during their marine life history stages (i.e. chinook salmon: Healey 1991, coho salmon: Sandercock 1991, Atlantic salmon: Mills 1989; Hislop and Webb 1992; Jacobsen and Hansen 2001). The fish species used in marine-based farms throughout most of the northern hemisphere are also piscivores. These include sea bass (*Dicentrarchus labrax*), sea bream (*Sparus aurata*) (Europe), cod (*Gadus morhua*) (Canada and Europe), sablefish (*Anoplopoma fimbria*) (Pacific Canada) and salmonid species, such as Atlantic (*Salmo salar*), chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*) and steelhead and rainbow trout (*O. mykiss*) (Canada, Europe, Chile, Australia). Such species are often opportunistic predators that consume a large variety of fish and plankton prey in nature and have recently been domesticated because of their high value, efficient feed / energy conversion and high growth rates (c.f. Naylor et al. 2000).

Johannes and Hay (2006) reviewed all the field studies that examined the direct predation effects of farmed fish in cages on wild fish and plankton communities near marine-based fish farm sites. Results compiled from these studies (Figure 1) indicated that the consumption of wild prey by caged salmon is often low (<5 wild prey per salmon) and limited to few wild fish (Pacific herring) and locally available plankton. Caged salmon rarely consumed wild fish attracted to cages (Johannes and Hay 2006) despite survey observations of high densities of juvenile pink and chum salmon, Pacific herring and sand lance which occur in proximity to cages in BC (Haegele et al. 1991).

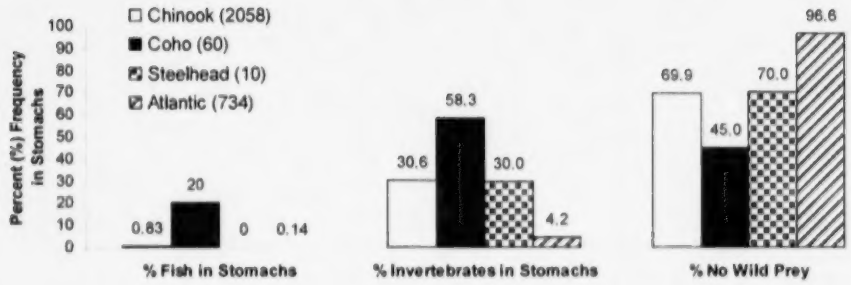

Figure 1. Summary of existing studies on wild prey consumption by caged salmon in British Columbia (sample sizes are given in parentheses).

Patterns and rates of wild prey consumption varied among and within salmon species and individuals within cages, and by season and farm sites (Black et al. 1992; Hay et al. 2004; Johannes and Hay 2006). Invertebrates abundant in the periphyton "fouling" community of cage netting were commonly consumed by all species of salmon. There was little evidence of fish or fish larvae in stomachs of caged salmon. Wild prey consumption by endemic farmed Pacific salmon species (Chinook, coho, steelhead) was higher relative to exotic Atlantic salmon. Coho salmon showed the greatest level of wild fish consumption. Higher site-specific consumption rates by chinook and coho salmon coincided with higher local densities of fish and plankton in the vicinity of farm sites. There was little available evidence to either support or refute the association between wild prey consumption by caged salmon and prey densities inside and outside cages, age of cages, level of fouling, or the frequency of cage cleaning. Hay et al. (2004) found no association between wild prey consumption and continuous lighting conditions around certain fish farm sites. Lighted conditions were expected to attract greater concentrations of potential wild prey to farms and enhance feeding opportunities by caged salmon.

Miller and Black (1992) and Black and Miller (1993) found evidence that farmed salmon in BC consumed wood and inorganic debris in the water column when cages were sited near industrial sources of logging debris (coastal pulp mills, log sort and dump sites). There was no evidence in the reviewed literature that adult wild fish (of a size comparable to those in these studies) consumed wood debris. Consumption of the wood debris was associated with a 4-fold increase in mortality and morphological changes in the stomach lining that were not seen at a farm site where sources of wood debris were absent. These observations suggest that farmed salmon may, to their detriment, learn a prey hunting image that orients the fish towards consumption of non-motile particles (similar to feed pellets) in preference to motile invertebrates and juvenile fish that occur in net cages (E. Black pers. comm.). Experience with commercial feed may be the dominant factor in fixing a learned hunting image for prey selection of cage reared fish. This hypothesis of the formation of a strong hunting image by caged salmonids would seem to be further supported by observations that in some locations juvenile herring would enter the salmon cages through the cage mesh, feed on the locally available pellets and grow to a size where they were unable to exit. In nature salmon commonly use herring as a prey item, yet in the cages when farmers undertook to sort or harvest their

salmon stock, the herring survival was such that considerable effort had to be made to sort numerous herring out of the cage (E. Black pers. comm.).

During normal finfish aquaculture operations, salmon are usually starved for 1 to 40 days prior to harvesting. Field studies showed that wild prey consumption by salmon declined initially while starved fish attempted to conserve energy, but that salmon starved more than 15 days showed an increase in consumption rate of wild fish and plankton (Figure 2). Johannes and Hay (2006) suggest that the timing and frequency of stomach sample collection could potentially produce low biased estimates of predation on wild fish and plankton by caged salmon. Analysis of >2500 salmon stomachs showed few or no observations of fish scales or fragments of wild fish as evidence of effects of predation by caged salmon (Hay et al. 2004, Johannes and Hay 2006). Stomach content weights of the farmed salmon examined did not meet levels of stomach fullness predicted to achieve observed growth and size of these fish. This suggests that the stomach samples were not representative of actively feeding caged salmon.

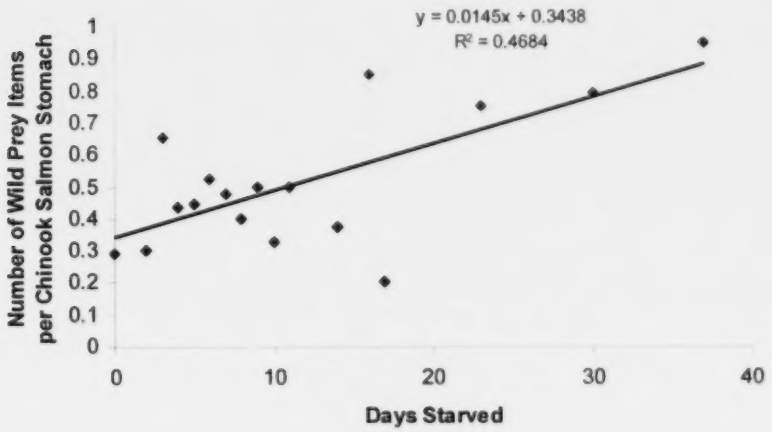

Figure 2. Linear association between mean wild prey items consumed by salmon and number of days starved prior to harvest. Taken from Figure 5, Johannes and Hay 2006.

This review suggests that caged salmon inconsistently eat wild prey at low rates and may have little direct predation effects on local or migrating wild populations of juvenile salmonids or pelagic forage fish species such as herring or eulachon in BC. Stomach content analyses indicate that the samples collected to date may not be adequate to reflect normal patterns of feeding and behaviour by caged salmon. Apart from the BC studies, no other information exists on direct predation between caged salmon and wild fish. There is a knowledge gap in the Canadian and international literature in this area of study. New study should be undertaken to examine the effect and relevance of caged finfish predation on wild fish and plankton prey in proximity to farm sites.

B. ATTRACTION TO FARM SITES

Fish cages and other artificial structures around marine aquaculture operations attract wild fish, plankton and settling invertebrates (Table 1). In some cases, artificial lighting used to extend the photoperiod for growing cultured fish may also enhance local attraction by wild fish and plankton to cages. Several explanations may account for increases in wild fish density, biomass or species composition in proximity to fish farms. First, wild pelagic and demersal fish are attracted to fish farms by enriched food supplies in the form of surplus fish food pellets and farm and fish waste. Second, cage facilities and structures act as artificial reefs to create and enhance shelter from predators and habitat complexity for wild fish and invertebrates (Dempster 2005). Complex habitats enhance abundance and growth of epifauna and epiphytic communities, which comprise a food source for wild fish. Third, accumulated sediments act to increase the benthic macrofauna abundance available as food for demersal wild fish (Pearson and Rosenberg 1978; detailed review in Hargrave 2003). Table 1 summarizes the literature on attraction of marine and freshwater wild fish to finfish cages and aquaculture sites, and classifies various studies based on the farmed and wild fish species and level of attraction.

A review of these studies illustrates four distinct levels (I–IV below) of attraction of wild fish to farm sites. The level of attraction appears related to biophysical conditions of the farm site.

I Cold water, northern marine farm sites (Norway, Scotland, Denmark) show that wild pelagic species such as saithe and whiting are attracted to fish farms by surplus farm pellets (Bjordal and Skar 1992; Bjordal and Johnstone 1993; Carss 1990; Christensen et al. 1991; and Skog et al. 2003). Carss (1990) and Christensen et al (1991) also suggest some limited response by demersal fish feeding on enriched benthic fauna. Cold water marine farm sites show a 5- to 15-fold increase in wild fish density and biomass, and a limited increase in fish community species composition. Boutillier (1996) found no attraction response from demersal prawn invertebrates to salmon farms in British Columbia.

II Warmer water, oligotrophic marine farm (Canary Islands, Spain, Greece, Italy) show a 10- to 1000-fold increase in wild fish density, biomass and species composition attracted to farm sites (Boyra et al. 2004; Dempster et al. 2002, 2004, and 2005; Machias et al. 2004, 2005; Sara et al. 2004; Vita et al. 2004). The level of attraction is attributed principally to responses by demersal wild species feeding on surplus pellets, fish waste and enriched macrobenthic fauna. Vita et al. (2004) and Felsing et al. (2005) also showed that demersal and pelagic wild fish species consumed greater than 40–80% of the surplus fish farm pellets and waste and cycled these back into the natural environment.

III Cold, brackish and freshwater farm sites (Finland, Norway, Great Lakes Canada) show a 1- to 10-fold increase in wild fish density and biomass attracted to farm sites (Björklund et al. 1990; Gabrielsen 1999; Henriksson 1991; Johnson et al. 2006; Koivisto and Blomqvist 1988). In most studies, little response was seen in the wild

fish community species composition. Wild pelagic and demersal fish were seasonally attracted to farm sites to feed on surplus pellets.

IV Warm freshwater farm sites (southern USA) show an increase in wild fish density and biomass attracted to catfish farm sites (Collins 1971; Hays 1980; Kilambi et al. 1978; Loyacano and Smith 1975). Wild pelagic and demersal fish species were seasonally attracted to cages to feed on surplus pellets and enriched benthic macrofauna.

The biophysical conditions, temperature and general productivity levels of coastal aquaculture sites are associated with the type and magnitude of attraction response by wild fish to farm sites. No studies have been conducted to explicitly examine wild fish attraction to farm sites in Canada. There is a knowledge gap in Canadian literature on this topic. Given the similarities between cold northern hemisphere marine aquaculture site conditions in Europe and Canada, we might predict wild fish in Pacific and Atlantic regions to show 1- to 10-fold increases in fish density and biomass due to attraction to farm sites, but show limited responses in community biodiversity. New study is needed in Canada to identify what factors influence attraction by wild fish populations to farm sites.

Table 1. Attraction of marine and freshwater wild fish to finfish cages and aquaculture sites.

Farmed Fish Species	Marine / Freshwater	Fish Farm Location	Fish Farm Effect on Wild Fish	Magnitude of Effect of Fish Farm	Major Wild Species*	Source
Atlantic Salmon	Marine	Norway	Food attraction – Saithe residence 1–7 months near farm sites.	Positive attraction and residence of pelagic fish feeding on surplus food at farm site.	Saithe	Bjordal and Skar 1992
Atlantic Salmon Cod	Marine	Norway	Food attraction – Daily patterns of saithe movement associated with farms sites.	Positive attraction to farm site by pelagic fish feeding on surplus food.	Saithe	Bjordal and Johnstone 1993
Atlantic Salmon & Rainbow Trout	Brackish Marine	Finland	Food and benthic fauna response. Transfer of oxytetracycline to wild fish in vicinity of farms.	Increased antibiotics in wild pelagic and demersal fish through direct transfer from surplus food and feeding on benthic fauna.	Bleak, Roach and Perch	Björklund et al. 1990
Atlantic Salmon	Marine	British Columbia	Annual catch trends showed no association with fish farm areas.	No change in prawn density and distribution.	Prawns	Boutillier 1996
Sea bream & Sea bass	Marine	Canary Islands	Food, shelter habitat and benthic fauna attraction. Coastal fish farms attract wild fish with higher species diversity and closer proximity of farm sites.	Positive, persistent attraction of 100 to 1000-fold higher density of wild pelagic and demersal fish species.	Boop, Pagellus	Boyra et al. 2004
Atlantic Salmon & Rainbow Trout	Marine & Freshwater	Scotland	Food attraction. Higher biomass and density of wild fish associated with fish farms. High frequency of wild saithe feeding on farm pellets. Other fish attracted to site, but not feeding on pellets.	Positive effect of 5- to 12-fold higher density and biomass of wild pelagic and some demersal fish species.	Saithe Various gadoids	Carss 1990
Rainbow trout	Brackish Marine	Denmark	Benthic fauna attraction. Higher catches of benthic oriented marine fish. Flounder consumed waste pellets from fish farm.	Positive effects 1- to 2-fold increase in fish biomass (catch) of wild demersal fish feeding on enhanced benthos in proximity of farm sites.	Flounder, Plaice	Christensen et al. 1991
Blue and Channel Catfish	Freshwater	USA	Food and benthic fauna attraction. Observed higher numbers of sunfish species in vicinity of cage sites.	Positive attraction of wild fish to cage sites.	Redear sunfish, bluegill.	Collins 1971

...cont.

Farmed Fish Species *	Marine / Freshwater	Fish Farm Location	Fish Farm Effect on Wild Fish	Magnitude of Effect of Fish Farm	Major Wild Species*	Source
Sea bream & Sea bass	Marine	Spain – SW Mediterranean	Significant attraction of wild fish to farm sites.	Strong positive increase in wild fish abundance, biomass and species composition in proximity to farm sites. 100- to 1000-fold higher wild fish.	Various species	Dempster et al. 2002
Sea bream & Sea bass	Marine	Spain – SW Mediterranean & East Australia	Food, habitat, and benthic fauna attraction. Significant attraction of wild fish to farm sites.	Strong positive increase in wild fish abundance, biomass and species composition in proximity to farm sites. 100- to 1000-fold higher wild fish.	Various species	Dempster et al. 2004
Sea bream & Sea bass	Marine	Spain - SW Mediterranean & Canary Islands	Food, habitat, and benthic fauna attraction. Significant attraction of wild fish to farm sites. Similar to Dempster et al. 2002 and 2004 above.	Strong positive increase in wild fish abundance, biomass and species composition in proximity to farm sites.	Various species	Dempster et al. 2005
Rainbow trout	Marine	Western Australia	Wild fish attracted to cages and were observed as a significant consumer of fish farm waste.	40–60% of total excess pellet or feces nutrients consumed by wild fish.	Unknown	Felsing et al. 2005
Atlantic salmon & Rainbow trout	Freshwater	Norway	Benthic fauna attraction. Increase in growth benthic oriented wild Arctic charr, rather than littoral – surface feeding brown trout. Charr were found to be fed on waste pellets.	Positive increase in demersal charr growth associated with farm waste and benthic fauna.	Arctic charr & Brown trout	Gabrielsen 1999
Catfish	Freshwater	USA	Food and habitat attraction. Attraction of wild fish to cage sites.	Higher numbers of wild species.	na	Hays 1980
Rainbow trout	Brackish Marine	Finland	Food and benthic fauna attraction. Attraction of wild fish to farm sites due to great food availability and enriched local conditions.	Positive increase 2- to 10-fold of wild pelagic and demersal fish species associated with fish farms.	Perch	Henriksson 1991
Rainbow trout	Freshwater	Lake Huron, CA	Food attraction. Attraction of wild fish to cage sites. Insignificant increase, although consistently observed in all species accept pelagic planktivore.	Positive increase by 10–20% in wild fish species associated with cage sites. No change in species diversity or composition near cage sites.	Spottail shiner	Johnson et al. 2006

...cont.

Farmed Fish Species *	Marine / Freshwater	Fish Farm Location	Fish Farm Effect on Wild Fish	Magnitude of Effect of Fish Farm	Major Wild Species*	Source
Rainbow trout & catfish	Freshwater	USA	Habitat and benthic fauna attraction. Increased populations of wild centrachids including bass and sunfish. Bass attracted to cage site to feed on abundant prey.	Positive increase in wild largemouth bass abundance and survival associated with cage sites.	Largemouth bass	Kilambi et al. 1978
Rainbow trout	Brackish Marine	Finland	Food, habitat. and benthic fauna attraction. General shift of wild fish communities to those dominated by juvenile and small fish species.	Positive increase in wild pelagic and demersal fish abundance, size and age and species composition associated with farm sites.	Roach, bream.	Koivston and Blomquist 1988
Channel catfish	Freshwater	USA	Food and habitat attraction. Higher biomass of catches of pelagic and benthic fishes in vicinity of catfish cage sites.	Positive effects 1- to 2-fold increase in fish biomass near cage sites. 20% increase in species diversity.	Gizzard shad	Loyacano and Smith 1975
Sea bream & Sea bass	Marine	Greece Aegean Sea	Food, habitat. and benthic fauna attraction. Higher abundance and species compositions surrounding fish farm sites. Larger area of influence due to low nutrients in area.	Four fold increase in species abundance and species composition in fish community.	Various demersal and pelagic species	Machias et al. 2004
Sea bream & Sea bass	Marine	Greece Aegean Sea	Food, habitat. and benthic fauna attraction. Higher abundance, biomass. and species diversity. Pronounced larger variation in wild fish population age and size distribution following period of recruitment.	Positive effects 2- to 3-fold increase in wild fish biomass, plus increase in local fish catch as landings. Large response of wild in region due to nutrient enrichment from fish farms.	Various demersal and pelagic fish species	Machias et al. 2005
Sea bream & Sea bass	Marine	Italy, Gulf of Castellammare	Food and benthic fauna attraction. Stable isotopes were used to identify and trace fish farm waste. Wild fish key in delaying and enlarging the deposition of fish farm waste material.	Positive effect of fish farm waste on wild fish populations. Wild increased deposition and range of fish farm waste	Various demersal and pelagic fish species	Sara et al. 2004
Atlantic salmon	Marine	Norway	Food attraction. Saithe grow faster and larger due high diet of fish farm pellets. Taste and fatty acid difference were detected.	Positive effect of fish farm food on growth and fat content of wild saithe.	Saithe	Skog et al. 2003

...cont.

Farmed Fish Species *	Marine / Freshwater	Fish Farm Location	Fish Farm Effect on Wild Fish	Magnitude of Effect of Fish Farm	Major Wild Species*	Source
Sea bream & Sea bass	Marine	Spain – SW Mediterranean	Food, habitat, and benthic fauna attraction. Large amount of food waste from fish farms provide a large source of food for wild fish.	Positive effect of fish farm food on growth of wild fish. Greater than 80% of waste food was cycled through wild fish.	Various demersal and pelagic fish species	Vita et al. 2004

*Fish species: Arctic charr *(Salvelinus alpinus)*, Atlantic salmon *(Salmo salar)*, Bleak *(Alburnus alburnus)*, Blue catfish *(Ictalurus furcatus)*, Bluegill *(Lepomis macrochirus)*, Boop *(Boops boops)*, Brown trout *(Salmo trutta)* Channel catfish *(Ictalarus punctatus)*, Chinook salmon *(Oncorhynchus tshawytscha)*, Cod *(Gadus morhua)*, Flounder *(Platichthys flesus)*, Gizzard shad *(Dorosoma cepedianum)*, Largemouth bass *(Micropterus salmoides)*, Pegallus *(Pagellus acarne)*, Perch *(Perca fluviatilis)*, Plaice *(Pleuronectes platessa)*, Prawn *(Pandalus platyceros)*, Rainbow trout *(Oncorhynchus mykiss)*, Redear sunfish *(Lepomis microlophus)*, Roach *(Rutilus rutilus)*, Saithe *(Pollachius virens)*, Sea Bass *(Dicentrarchus labrax)*, Sea bream *(Sparus aurata)*, Spottail shiner *(Notropis hudsonius)*

C. RESOURCE COMPETITION AND PREDATION BY ESCAPED FARM FISH AND WILD FISH IN MARINE ENVIRONMENTS

Little study has been conducted on the effects of resource competition and predation between escaped farm fish and wild fish populations in marine environments (ICES 2005a). The available literature indicates that the level of the effect of escaped fish is linked to their numbers and to whether they are endemic (native) or exotic (non-native) to the farm area. These factors are important in respect of their ability to develop a wild-type feeding behaviour following an escape event (Gross 1998). Atlantic and Pacific salmon are farmed in regions where they are endemic (Atlantic salmon in Scotland, Ireland, Iceland, Norway, Atlantic US and Canada; Pacific salmon in Pacific US and Canada) and also in regions where they are exotic (Atlantic salmon in Pacific US and Canada, Chile; Pacific salmon in Norway Scotland, Chile, New Zealand, Australia). Similarly, non-salmonid species are gaining popularity for culture, but are currently exclusive to regions in which they are an endemic species (halibut, pilchard and sablefish in Pacific Canada; sea bream, sea bass in the Mediterranean; cod and turbot in the North Atlantic).

Research on the interactions of escaped farmed salmon and wild fish has focused on genetics and hybridization, disease and parasite transfer, and competition between escaped farm and wild salmon as freshwater spawners and juveniles in regions where farmed fish are endemic (North Atlantic e.g. Norway, Sweden, Atlantic US and Canada) (Weir and Grant 2005; Weir and Fleming 2006). This report does not review this literature as it has been reviewed in another State of Knowledge report (Weir and Fleming 2006). This report focuses on the potential interactions and effects of escaped farmed fish on wild fish populations in marine environments. Few studies have examined competition for food, space and reproductive success, or predation effects between escaped exotic farmed fish and native wild fish (e.g. Atlantic salmon escapes in Pacific ocean: McKinnell and Thomson 1997; Atlantic and Pacific salmon escapes in the southern Pacific ocean: Soto et al. 2001). Still fewer studies have examined the competition and predation interactions between either endemic or exotic escaped farmed salmon and wild fish in marine systems, or other escaped non-salmonid farmed species such as sea bream, sea bass, turbot (*Psetta maxima*) (ICES 2005a), cod, sablefish and halibut and wild fish. For example, Soto et al. (2001) conducted extensive fish surveys in the inner seas and fjords of Chile in response to greater than 4 million escaped farmed salmon between 1994 and 1995. Chilean artisanal fisheries had observed large reductions in native fish abundance and catch, and requested that a salmon fishery be established in response to high by-catches of exotic salmon. Soto et al. (2001) showed that native fish numbers and diversity were strongly depressed in association with increased abundance of escaped salmon (Figure 3). Their results suggested the importance of examining first competitor and second predator effects of escaped salmon on wild fish populations. In Canada, continued incidents of escaped exotic or endemic farmed salmon in BC and Atlantic Canada stress the need to understand the potential for adverse effects on wild fish populations.

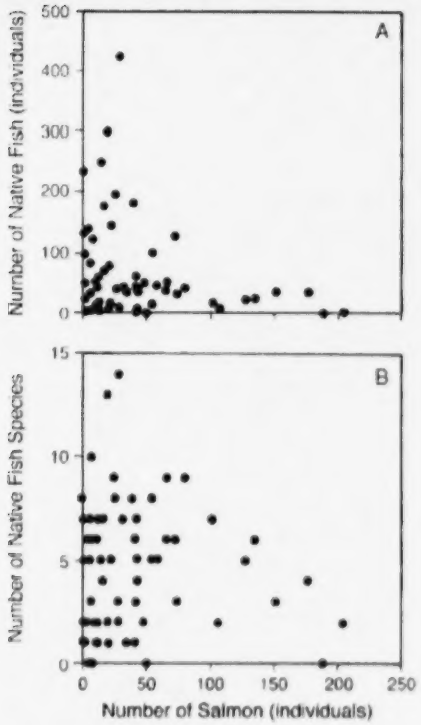

Figure 3. Association between catch of escaped Chilean farmed salmon and native Chilean fish numbers (A) and native fish species diversity (B). From Soto et al. 2001.

Levels of escaped salmon are not well documented in Atlantic Canada but isolated incidental reporting has estimated escapes at ~10% of wild salmon freshwater annual returns (100,000 to 300,000 wild salmon) or about 10,000 to 30,000 farmed salmon escapes per year (Ritter et al. 1999). In some instances, escaped farmed fish have been shown to outnumber wild fish populations (i.e. Norway Gausen and Moen 1991, Saegrov et al. 1997; Scotland: Webb et al. 1999; New Brunswick: Carr et al. 1997, Ritter et al. 1999; Chile: Soto et al. 2001; Maine: Goldberg et al 2001). More than 80% of the Atlantic salmon caught in the Faroes of the Northeast Atlantic Ocean and the Baltic sea are of farmed origin (Hansen et al. 1993, 1997; Crozier 1998, Hansen et al. 1999). In BC and Washington, >1,000,000 each of farmed Pacific and Atlantic salmon have escaped during the 1987 to 2002 interval (Figure 4, Table 2). Currently the estimated average number of salmon escapes per year comprise a small fraction (<0.01%) of the total number of wild Pacific salmon in Canada and US (Fisheries and Oceans Canada 2001, Augerot and Foley 2005). Events like storm, boat or predator induced net / cage failures often allow large numbers of farmed salmon to escape over restricted areas and time periods (Whoriskey 2001; BC Ministry of Agriculture, Food and Fisheries 2004) and may have concentrated local effects on wild fish populations. In BC, growing concerns about the relative increased abundance of hatchery versus wild Coho salmon (Sweeting et al. 2003; Beamish et al. 2004) and aquaculture escapes (Morton and Volpe 2002) in the

Strait of Georgia have heightened interest in understanding potential interactions and effects of escaped salmon with wild salmon populations. These issues are also intensified by trends that suggest that >8% of the Pacific salmon stocks are extinct or at high risk of extinction (Slaney et al. 1996) and that their survival is potentially affected by human-induced stressors including land use, commercial fisheries, climate variation and fish culture and enhancement activities.

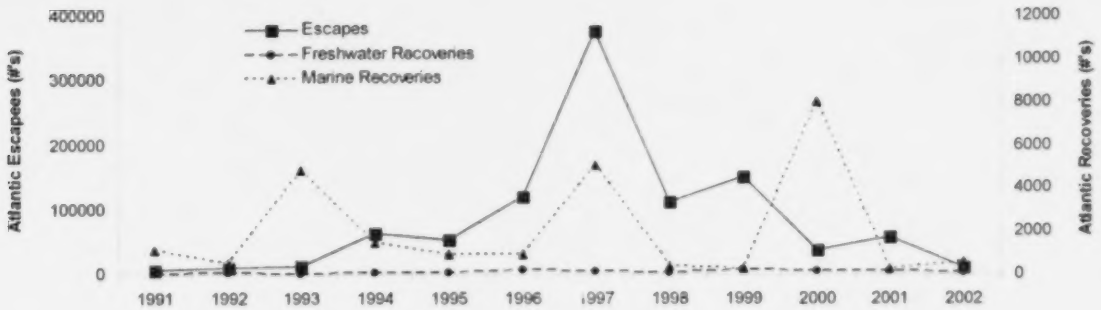

Figure 4. Estimated total Atlantic salmon escapes, marine and freshwater recoveries from Washington, British Columbia and Alaska. Source: Fisheries and Oceans Canada Atlantic Salmon Watch Program www.pac.dfo-mpo.gc.ca/sci/aqua/ASWP_e.htm (accessed 23 May 2006).

Table 2. Summary of percent difference in numbers of escaped Atlantic salmon relative to marine and freshwater recoveries in B.C., Washington and Alaska. Source: Fisheries and Oceans Canada Atlantic Salmon Watch Program at: www.pac.dfo-mpo.gc.ca/sci/aqua/ASWP_e.htm (accessed 23 May 2006).

Year	Total Pacific Salmon Escapes	Total Atlantic Salmon Escapes	% Marine Recovery (Atlantic Salmon)	% Freshwater Recovery (Atlantic Salmon)
1987	54998	Unknown	–	–
1988	2000	Unknown	–	–
1989	392271	Unknown	–	–
1990	165000	unknown	–	–
1991	229500	6651	16.0	0.12
1992	59632	9544	5.0	0.50
1993	12113	11500	42.0	0.20
1994	2300	63929	2.3	0.08
1995	6000	51883	1.8	0.11
1996	0	120104	0.8	0.18
1997	38956	376471	1.3	0.03
1998	1900	111607	0.3	0.08
1999	0	150740	0.1	0.12
2000	36392	37392	21.4	0.35
2001	0	57643	0.4	0.20
2002	9198	9282	6.1	0.43
2003	Unknown	Unknown	–	–

Limited observations exist on both the survival (Tables 2 and 3 and Figures 4 and 5) and feeding behaviour (Table 4) of escaped farmed fish in marine systems; both data types are needed to examine the magnitude of potential effects of escaped farmed fish. The most comprehensive data on numbers and survival of escaped salmon and feeding behaviour are from Thomson and McKinnell (1993 to 1997), Thomson and Candy (1998), in BC, and Soto et al. (2001) in Chile. Feeding behaviour and stomach contents have been assessed in the Northeastern Atlantic Ocean (Norway, Scotland, Iceland), but feeding patterns are not linked to the number or survival of escaped farm fish (Hislop and Webb 1992; Hansen et al. 1993, 1997; Crozier 1998; Hansen et al. 1999; Jacobsen and Hansen 2001; Hansen and Jacobsen 2003).

In BC, <5% of escaped Atlantic salmon were recovered in the marine environment and <0.3% were recovered in freshwater (Table 3; for details see Burt et al. 1992; Thomson and McKinnell 1993, 1994, 1995, 1997; and Thomson and Candy 1998). These recovery rates suggest annual extrapolated estimates of <5000 Atlantic salmon escaped to marine environments and <200 to freshwater environments. Observations of the escaped salmon capture location also suggest that farmed fish have limited distribution beyond farm sites (10–50 km) in BC. Observations of escaped farmed salmon in the Northeastern Atlantic Ocean suggest that farmed salmon distribute over much greater areas than those observed in B.C. Marine and freshwater recoveries in BC, classified by geographic location (Table 1), indicate the highest proportion of escaped salmon were captured in northeast and west coast Vancouver Island and Washington in areas with the largest concentrations of salmon farms. Marine and freshwater counts of escaped salmon in BC are not comprehensive. Although reporting of Atlantic salmon captured in commercial fisheries is required by licence, present fisheries in BC are spatially and temporally restricted and do not provide comprehensive monitoring of escaped Atlantic salmon (i.e. Morton and Volpe 2002). Accuracy of marine farmed fish escape and recovery estimates is also constrained by the extent of fish distribution and surveys in the ocean and freshwater, the spatial extent of available wild salmon habitat, and by limited or inaccurate information about cause, timing, and numbers of escaped farm fish (Norway: Gausen and Moen 1991, Heggeberget et al. 1993; Europe: Crozier 1998, Hansen and Jacobsen 2003; Canadian Maritimes: Lacroix and Fleming 1998, Ritter et al. 1999; US East Coast: FWS / NOAA 2000; Chile: Soto et al. 2001; Canadian West Coast: McKinnell et al. 1997, McKinnell and Thomson 1997, Morton and Volpe 2002).

Table 3. Summary percent frequency of marine and freshwater recoveries by region from south to north in Washington, British Columbia, and Alaska averaged across all years. Information for Washington State freshwater recoveries not available.

Area	Marine Recoveries	Freshwater Recoveries
Washington (Puget Sound)	20.9	n/a
North East Coast Vancouver Island	70.0	52.9
West Coast Vancouver Island	3.3	45.9
Central – North Coast BC	2.1	0.8
SE Alaska	0.6	0.3
Northern Alaska	1.8	0
Gulf of Alaska	1.2	0

The final component examined on the interaction of escaped salmon and wild fish was a review of feeding behaviour and prey preferences in marine environments. These studies showed that escaped Atlantic salmon in the Northeastern Atlantic, where they are endemic, reverted to feeding behaviours and diets similar to those of wild salmon (Table 4) (Hislop and Webb 1992; Hansen et al. 1997; Jacobsen and Hansen 2001). These data also suggested that most escaped fish become piscivorous once acclimated to the wild, whether they are endemic or exotic. In Chile, all escaped salmon prey types (pelagic planktivorous fish) were consistent with those chosen by wild salmon in their native environments. Escaped coho salmon reverted quickly to piscivorous feeding behaviour in the wild (Soto et al. 2001) and in some cases while still caged (Johannes and Hay 2006). Escaped Atlantic salmon in BC are an exception and did not revert to a feeding behaviour consistent with either wild Pacific or Atlantic salmon. Wild fish prey such as herring and sand lance were observed in stomachs of escaped Atlantic salmon in BC but at lower occurrences than those of wild fish. The incidence of empty stomachs in BC escaped Atlantic salmon was also consistently higher than in other regions of fish farms in the world. Additional evidence showed that fat content of escaped Atlantic salmon differed between BC and more distant Alaska areas of capture (Figure 5). These data suggested that escaped fish are losing fat reserves gained during their farm residence as they distribute farther from areas of fish farms without an effective ability to feed in the wild. The diminished ability of escaped Atlantic salmon in BC to feed in the wild may be a corollary of post-introduction domestication in these strains of salmon (H. Kreiberg pers. comm.).

Table 4. Summary of literature on escaped (endemic or exotic) and wild salmon feeding and prey preferences. Percentage estimates of empty stomachs, stomachs with fish and invertebrate prey and pellets, based on numbers of stomachs sampled.

Salmon Species	Endemic or Exotic Cultured / Wild	Location*	n	Salmon Length Range (cm)	% Empty Stomachs	% Fish Prey	% Invertebrate Prey	% Farm Pellets	Preferred Fish Prey Species**	Source
Atlantic	Endemic	SC	54	49–80	64.8	31.5	7.4	0	Sandeel, Whiting	Hislop & Webb 1992
Atlantic	Endemic	NWY	863	42–100	24.9	3.7	71.1	0	Pearlside, Lanternfish, Herring	Jacobsen & Hansen 2001
Atlantic	Exotic	Ch	189	40–90	65.6	8.6	10.6	15.2	Unknown	Soto, et al. 2001
Coho	Exotic	Ch	803	40–70	41.0	22.8	27.6	8.6	Anchovy, Sardine, Mote, Sliversides	Soto et al. 2001
Rainbow Trout	Exotic	Ch	526	20–70	39.1	15.2	37.1	8.6	Unknown	Soto, et al. 2001
Atlantic	Exotic	BC	1		100	0	0	0	Not applicable	Burt et al. 1992
Atlantic	Exotic	BC	59		98.3	1.7	0	0	Herring	Thomson & McKinnell 1993
Atlantic	Exotic	BC	143	41–95	93.0	2.1	0	4.9	Herring	Thomson & McKinnell 1994
Atlantic	Exotic	BC	106	53–71	95.3	2.8	1.9	0	Herring	Thomson & McKinnell 1995
Atlantic	Exotic	AK	23	51–75	91.3	8.7	0	0	Herring	Thomson & McKinnell 1995
Atlantic	Exotic	BC	146	52–83	86.3	10.3	2.1	1.4	Herring	Thomson & McKinnell 1996
Atlantic	Exotic	AK	13	47–82	92.3	7.7	0	0	Herring	Thomson & McKinnell 1996
Atlantic	Exotic	BC	111	53–78	92.8	1.8	4.5	0.9	Herring	Thomson & McKinnell 1997
Atlantic	Exotic	AK	131	46–83	91.6	3.8	4.6	0	Herring, Sand lance	Thomson & McKinnell 1997
Atlantic	Exotic	BC	133	47–80	96.2	1.5	0	2.3	Herring	Thomson & McKinnell 1998
Atlantic	Exotic	AK	73	35–82	87.7	9.6	2.7	0	Herring, Sand lance	Thomson & McKinnell 1998
Atlantic	Exotic	AK	1	58	0	0	100	0	Not applicable	Brodeur & Busby 1998
Atlantic	Exotic	BC	775	56–89	95.4	1.7	0.6	1.4	Herring, salmon sp., Sand lance	Morton & Volpe 2002

Con't ... Salmon Species	Endemic or Exotic Cultured / Wild	Location*	n	Salmon Length Range (cm)	% Empty Stomachs	% Fish Prey	% Invertebrate Prey	% Farm Pellets	Preferred Fish Prey Species**	Source
Chinook	Wild	BC		n/a	~20-50	40-65	0	n/a	Herring, Sand lance	Healey 1991
Coho	Wild	BC		n/a	~20	~70	~10	n/a	Herring, Sand lance	Waddell et al. 1992
Atlantic	Wild	NWY	1929	40–110	32.1	3.3	64.5	n/a	Pearlside, Lanternfish, herring	Jacobsen & Hansen 2001

*Locations: SC – Scotland, NWY – Norway and Norwegian Sea, CH – Chile, AK – Alaska, BC – British Columbia
**Anchovy – *Engraulis* ringens, Herring - *Cluepea harengus* and *Clupea harengus pallasi*, Lanternfish – *Lampanyctus crocodiles, Benthosema glaciale*, Mote – *Normanichthys crockery*, Pearlside – *Maurolicus muelleri*, Sandeel – *Ammodytes tobianus*, Sand Lance – *Ammodytes hexapterus*, Sardine – *Sardinops* sagax, Whiting – *Merlangius merlangus*

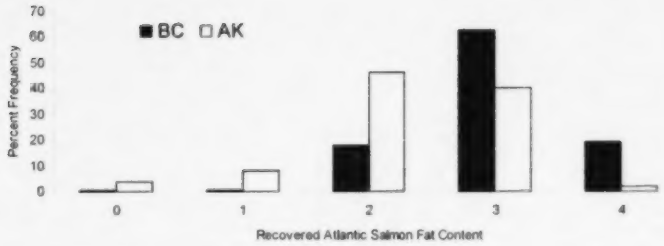

Figure 5. Summary of fat content from individual escaped Atlantic salmon recovered from British Columbia and Alaska. Fat content was visually assessed using a qualitative scale from 0 to 4. Data and methods are summarized from 1993–97 and from 1995–97 from BC and Alaska respectively (Thomson and McKinnell 1994, 1995, 1997, and Thomson and Candy 1998). BC salmon sampled = 642, Alaskan recovery salmon sampled = 199.

The existing literature suggests three patterns of interaction between escaped farmed fish and wild fish. First, Soto et al. (2001) demonstrated that very high densities of escaped fish are negatively associated with the abundance and diversity of wild fish, and escaped fish act as both competitors and predators. Second, evidence from lower densities of locally escaped farmed fish is inconclusive. There is a knowledge gap in the information about local interactions of escaped fish and wild fish and prey abundance and diversity. Escaped fish do revert to wild-type feeding behaviour, and given the magnitude of escaped fish numbers, time frame and spatial extent, it is conceivable that escaped fish could both prey upon and compete with local wild fish populations. Third, BC farmed Atlantic salmon do not feed on wild prey or fish as readily as do Atlantic salmon escaped in Chile or in Europe.

Limited data exist on the number, local distribution and feeding behaviour of escaped farmed fish and potential interactions with wild fish. New study on the abundance / survival and feeding / growth of escaped farmed fish is needed to quantify potential interactions and magnitude of effects on wild fish populations. There is a knowledge gap in both Canadian and international literature in this area of research into salmon aquaculture and non-salmonid cultured species like sablefish, halibut and cod.

GAPS IN KNOWLEDGE

A. PREDATION EFFECTS ON WILD FISH

New studies are required to determine if caged marine finfish (salmon and other cultured fish species like sablefish, cod, halibut) feed on local wild populations of plankton and fish. These studies should examine local and regional scales of influence between farmed finfish and wild fish populations to determine the relevance of this interaction.

- Early studies on consumption of wild prey by caged salmon in BC need to be replicated in BC and in the Maritime provinces of Canada. New experimental design for these studies should consider: site placement, finfish species, salmon species and strain, time of year (size / growth of finfish) and time of day (diel feeding cycle) for stomach sample.
- New studies should pair sampling of caged finfish with in situ sampling of wild fish and plankton in proximity to farm sites to examine potential trophic level interactions and magnitude and relevance of effect of farmed finfish on wild fish and plankton.
- New studies should consider the relevance of oceanographic physical and chemical conditions (including currents and tides) on trophic level interactions between farmed finfish and wild fish populations.
- Sample collections (timing – month, 24 hours) inside and outside of cages sites should consider important life history stages and concentrations of local wild fish populations i.e. migration corridors for juvenile salmonids, spawning times (salmon, herring).

B. ATTRACTION TO FARM SITES

New studies are required to determine the level and type of attraction by wild marine fish to finfish farm sites in Canada.

- No Canadian (northern temperate) studies in marine environments have examined the causes or consequences of attraction of wild fish to fish farms.
- What are the levels of attraction by wild fish to finfish aquaculture sites? Do farm sites compare to artificial reef structures?
- Do demersal fish species experience positive or negative increases in abundance associated with enhanced local food (pellet) availability?
- Do cage facilities locally establish shelter as artificial reefs and enhance local abundance of epifauna and epiphytic communities? Are potentially enhanced benthic macrofauna used as food for wild fish populations and does this stimulate attraction to cage sites?
- Local attraction of wild fish can influence potential transfer of parasites, disease or administered antibiotics; what is the risk of this transfer to and from wild fish population associated with their attraction and use of farm sites?
- What are the biophysical conditions in and around farm sites and do these influence the level of attraction and wild fish / plankton community productivity?
- Do varying culture practices or cultured species influence the level wild fish attraction?
- Are other finfish and shellfish polyculture options viable in various regions of Canada as trialed in the Maritimes (mussels and finfish)?
- Are other fisheries and marine resource use options viable in association with farm site through attraction and enhancement of local wild fish populations?

C. RESOURCE COMPETITION AND PREDATION BY ESCAPED FARM FISH AND WILD

New studies of escaped finfish into natural environments are required to link cause and consequences for wild fish and their ecosystems at both local and regional scales. Comprehensive monitoring, incident investigation and reporting are required to clearly establish the timing, quantities, species and condition of escaped farmed fish into the wild. New study is needed to establish the potential magnitude and relevance of escaped farmed fish competition and predation on wild fish populations.

- Monitoring activities on the fate of escaped farmed fish are incomplete in BC and poorly known in the Maritime provinces. Additional assessments are required to establish survival rates of escaped farm fish (all exotic and endemic species) in BC and the Maritime provinces. Beyond investigating escape incidents (BC), monitoring, assessment and reporting of escaped farmed fish often are only coincident to fisheries and normal assessment of wild fish populations (i.e. reporting in commercial salmon fisheries and river salmon spawner enumeration etc). Consideration should be given to assess distribution, abundance and survival of escaped endemic and exotic farmed fish to predict the relative competitive or predatory effects on wild fish populations.
- New study of escaped farmed fish is required to determine feeding and dispersion behaviour, survival and growth. Study design should incorporate the variety of farmed fish species, time of day and year, and farm site location.
- What are the local and regional consequences of escaped farmed fish to wild fish abundance and ecosystem biodiversity? Are these events and related consequences dependent on quantities, types of escaped fish?
- New studies should pair sampling at local farm sites and at larger regional ecosystem scales with sampling for wild fish, plankton at similar scales. What are the biophysical conditions around farm sites and at the regional level of ecosystems and do these influence the level of survival of escaped farmed fish, and the potential effects of escaped fish on local wild fish communities?
- New studies should consider the relevance of oceanographic physical and chemical conditions (including currents and tides) to examine the influence and contribution of variation in these conditions on trophic level interactions between escaped farmed finfish (survival, growth) and wild fish populations.

GENERAL KNOWLEDGE GAPS

Trophic Interactions between farmed fish and wild marine fish

- New studies must consider alternate experimental designs to examine trophic level interactions between farmed finfish and wild fish populations at a variety of local and regional scales. Experimental or adaptive management approaches should be considered to provide a range of risk exposure of finfish aquaculture on wild fish populations to reflect growing experience and understanding.

- Creative management approaches should be explored to provide positive options for selective fisheries or polyculture around farm sites due to attraction and enhancement (i.e. enhanced nutrients, wild fish abundance and biodiversity)
- Assessment of farmed finfish interactions with natural environments should identity and incorporate key indicators species to appraise the effects of caged finfish predation, attraction to farm sites and potential competition and predation by escaped farm fish.
- New study is needed to directly compare and contrast the diets of caged, escaped or wild salmon with the distribution of available food organisms and environmental conditions in marine environments.
- A Canadian working group should be convened to appraise and integrate the relative risks of farmed finfish to wild fish populations across the multiple issues identified here and in other State of Knowledge reporting (e.g. caged finfish predation, farm site attraction, competition / predation by escaped finfish, behavioural interactions, disease / parasite transfer, nutrient / productivity changes, ecosystem biodiversity, fish for fish food etc). New studies should prioritize research and management actions based levels of perceived risk to wild fish populations and local ecosystems. The objective of this research should be to evaluate and quantify the risk (Hargrave et al. 2005).

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